DUSKY DOLPHIN (*Lagenorhynchus obscurus*) UNDERWATER BAIT-BALLING BEHAVIORS AND ACOUSTIC SIGNALS: A COMPARISON BETWEEN ARGENTINA AND NEW ZEALAND

A Dissertation

by

ROBIN LEA VAUGHN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2011

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Bernd Würsig
Committee Members,	Jimmie Killingsworth
	Christopher Marshall
	Jane Packard
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ABSTRACT

Dusky Dolphin (*Lagenorhynchus obscurus*) Underwater Bait-Balling Behaviors and Acoustic Signals: A Comparison Between Argentina and New Zealand. (August 2011)

Robin Lea Vaughn, B.A., Miami University; B.S., Adams State College

Chair of Advisory Committee: Dr. Bernd Würsig

I characterized dusky dolphin (*Lagenorhynchus obscurus*) underwater bait-balling behaviors and acoustic signals, and compared data between Argentina and New Zealand (NZ) to investigate the roles of ecology versus social learning. I quantified prey herding and capturing behaviors from video footage, and I analyzed acoustic signals from narrowband recordings. In both locations, I related bait-balling behaviors and acoustic signals to group and prey ball sizes. In NZ, I also related dolphin behaviors to prey ball escape behaviors and acoustic signal parameters to examine proximate functions.

Observed herding behaviors typically involved dolphins swimming around or under a prey ball using a side body orientation, while dolphins typically captured fish from the side of a prey ball using a ventral orientation. Coordinated prey-capture behaviors may have made it easier for dolphins to capture fish by trapping fish between dolphins. Signals were categorized as click trains, burst pulses, and combinations due to a bimodal inter-click interval distribution. I observed 3 whistle-like chirp-screams, but no whistles. Sequences of burst pulses also occurred that contained 2-14 burst pulses that

aurally and visually appeared closely matched. Similarities between locations suggest that ecological context related to broad behavioral and acoustic parameters, while social learning differences may occur on a finer scale.

In NZ, prey balls exhibited horizontal and vertical movements, but the only behavior that preceded escape was "funneling", the brief formation of a ball shape where the height was at least twice the width. Dolphin behaviors that related to prey balls ascending were type of herding pass, location of prey-capture attempts, and body orientation during attempts. These behavioral parameters may also be used to counter vertical prey escape behaviors.

In NZ, all signal categories had a direct or indirect role in capturing prey. Click train-burst pulses were likely used for echolocating on prey, burst pulses and sequences appeared to have communication roles, and the role of click trains was ambiguous. No signal categories appeared to have a herding function, but the sheer number of signals emitted may have caused fish to cluster together more tightly and therefore facilitated capture.

For the oceans and their inhabitants,

And in loving memory of Violet and Lavendar

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CHAPTER I

INTRODUCTION

Dolphin foraging

Foraging includes the stages of locating, containing, and capturing prey (Wells et al. 1999; Heithaus and Dill 2009). Delphinids locate prey perhaps most often by echolocation or vision, but also via other senses such as hearing (Gannon et al. 2005). At times they need to contain this prey, either to prevent its escape or to make it easier to capture. Behaviors used to contain prey include swimming in circles around it (Clua and Grosvalet 2001), blowing bubbles (Similä and Ugarte 1993), slapping tails or bodies onto the water at the edge of the prey ball (Fertl and Würsig 1995), and driving prey towards a barrier such as other dolphins or the shore (Gazda et al. 2005). Containing prey typically occurs prior to capturing prey, e.g., when dolphins drive fish against a sandy beach so that they can capture them more easily. However, it can also occur concurrently with prey capture such as when dolphins capture fish at the bottom of a prey school, causing the prey to move closer to the surface. Dolphins typically capture prey one-at-a-time, and they often need to capture these individuals from within a rapidly moving fish school. They most commonly consume fish or squid, although larger delphinids such as killer whales (*Orcinus orca*) also eat dolphins, pinnipeds, sharks, and other types of marine fauna.

Ecological context determines which foraging behaviors are most effective for

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This dissertation follows the style of Behavioral Ecology.

locating, containing, and capturing prey. In shallow waters off the Florida Keys, bottlenose dolphins (*Tursiops* spp.) used their tails to create plumes of mud (Lewis and Schroeder 2003), in which prey became concentrated. In contrast, in the northern Gulf of Mexico where shrimp boats operate, bottlenose dolphins took advantage of trawling nets by feeding on the organisms that were stirred up by the nets (Leatherwood 1975). Within the same habitat, foraging behaviors and decisions can vary due to seasonal (or other) changes in prey or predators, which can affect behavioral costs and benefits. In Golfo San José, Argentina, dusky dolphins (*Lagenorhynchus obscurus*) coordinated behaviors to herd schools of anchovies (*Engraulis anchoita*) to the surface spring-fall, but during winter they fed individually on fish at greater depths (Würsig and Würsig 1980). As a second example, in Shark Bay, Australia, bottlenose were less likely to forage in prey rich environments when greater numbers of tiger sharks (*Galeocerdo cuvier*) were present (Heithaus and Dill 2006).

Social learning also influences delphinid foraging tactics (Rendell and Whitehead 2001; Whitehead et al. 2004). It has been hypothesized that dolphins learn some foraging behaviors by observing or being taught by their mother (i.e., vertical learning) or peers (i.e., horizontal learning), and this learning would be expected to take longer for more complex foraging behaviors. Off the Crozet Archipelago, evidence suggests that young killer whales learn from their moms how to beach themselves to catch elephant seal (*Mirounga leonina*) pups (Guinet 1991; Guinet and Bouvier 1995), a process that can take several years. In Shark Bay, Australia, vertical transmission of sponge carrying behaviors appears to occur from mother bottlenose dolphins to offspring (Sargeant and

Mann 2009). This behavior involves dolphins carrying sponges on their rostrums, and the sponges may protect dolphins' rostrums as they probe the substrate for prey. It has also been hypothesized that dolphins learn how to forage from peers, or that they refine foraging behaviors later in life via horizontal learning (similar to apparent horizontal transmission of "lobtail feeding" in humpback whales, *Megaptera novaeangliae*, Weinrich et al. 1992).

Coordinated foraging

Delphinids frequently coordinate behaviors to forage effectively, and this coordination can make it easier for them to locate, contain, or capture prey (Figure 1; Wells et al. 1999; Connor 2000; Heithaus and Dill 2009; Vaughn et al. 2010a). To search for prey more efficiently over a large area, a group may spread out in a line formation (Würsig 1986). To effectively contain prey in a horizontal direction, a driver bottlenose dolphin may herd fish against barrier dolphins (Gazda et al. 2005). To contain prey in a vertical direction, dolphins may alternate who is swimming around and under a prey ball by diving to depth in sequential fashion (similar to Baird and Dill 1995). During prey captures, coordinated behaviors may reduce the "confusion effect", which is a visual effect experienced by a predator looking at a school of fish whereby it is hard for to the predator to focus on an individual fish to capture it due to the visually confusing stream of fish that are continually moving by its eyes (Norris and Schilt 1988). Coordination of prey captures may make it easier for a dolphin to focus on and capture an individual fish or other prey item. For example, killer whales off Norway coordinate prey-capture behaviors by one whale slapping a herring school with its tail to stun fish,

then a different whale at times will capture the stunned fish (Similä and Ugarte 1993). Atlantic spotted dolphins (*Stenella frontalis*) in the Gulf of Mexico coordinate prey-capture behaviors at times by using bubbles in coordinated fashion to separate individual fish from schools just prior to prey-capture attempts (Fertl and Würsig 1995).

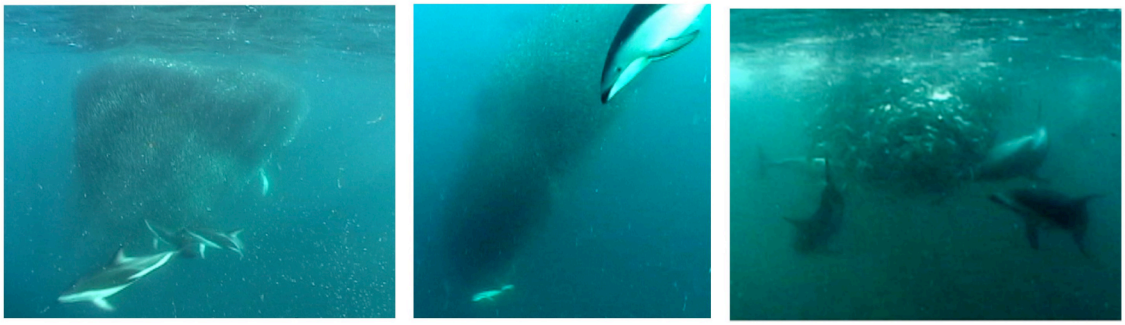

Figure 1. Examples of coordination by dusky dolphins (*Lagenorhynchus obscurus*) during prey containment and capture. Left photo shows dolphins surrounding prey balls to keep them stationary or at the surface, center photo shows dolphins diving to the bottom of a prey ball in sequential fashion to prevent it from descending, and right photos shows dolphins sandwiching a prey ball between individuals to facilitate capturing fish.

Relative costs and benefits of coordinating behaviors to locate, contain, or capture prey in different-sized groups (or individually) vary according to foraging tactic and ecological context (Heithaus and Dill 2009). In general, theory suggests that it is harder to locate prey when it is distributed more patchily or when fewer dolphins are searching (Norris and Dohl 1980). It appears to be more difficult for predators to contain prey when it is present in larger patches (Norris and Schilt 1988), when other disruptive predators are present (e.g., plunge-diving gannets, *Morus serrator*; Vaughn et

al. 2010b), or when fewer dolphins are present (Würsig and Würsig 1980). Prey capture has been hypothesized to be more difficult when prey is more elusive (e.g., faster swimming, more maneuverable; Würsig 1986), or present in a larger school (Vaughn et al. 2010a). Individual dolphins thus may forage in groups to reduce proximate costs, but group size may be limited by patch size due to competition for prey.

When dolphins contain or capture prey in groups, they may also be able to more efficiently coordinate behaviors when the group consists of individuals who are more familiar with each other, for example due to long-term associations (similar to Ramp et al. 2010). Formation of dolphin groups is often based on age, size, sex, or kinship (Shelton et al. 2010), and these groups at times contain long-term companions. Long-term relationships can be important in a mating context (e.g., for male alliances of bottlenose dolphins in Shark Bay, Connor et al. 2000), and likely also in a foraging context. Dusky dolphins do have preferred companions (Pearson 2008), and they have been observed with the same companions over as long as 8 years (Würsig and Bastida 1986).

From a conservation perspective, the potential importance of close or long-term associations to efficient foraging and mating means that it is probably not sufficient to focus on just the number of individuals present in a population. Instead, it is likely also important to conserve the intactness of social units within the population. Although our understanding of dolphin sociality is increasing, we still know little about the role and importance of different types of relationships in a foraging context. An important step in understanding this aspect of dolphin social life is to describe and quantify types of

coordination that occur during foraging, as well as how these behaviors are mediated via acoustic and non-acoustic communication.

Communication: how do dolphins coordinate behaviors during foraging?

Coordination of behaviors during foraging requires acoustic or non-acoustic communication, which can be defined as "a process by which a sender produces a signal, which alters the probability of a subsequent behavior in a receiver(s)" (Dudzinski et al. 2009). Communication may help individuals to synchronize prey herding or capturing behaviors and convey foraging decisions. It may also help them to coordinate concurrent or sequential behaviors so that they do not, for example, all attempt to capture a fish from a given prey ball at the same time. It is often difficult to determine how dolphins communicate (e.g., what categories of acoustic signals are used), and it is more difficult to understand particular communication roles of acoustic signals. However, one method that we can use to examine questions pertaining to functions of acoustic signals (or non-acoustic signals) is to relate signals to behaviors (e.g., Janik 2000a; Simon et al. 2006).

Dolphin acoustic signals, which I investigate in this dissertation, consist of click and whistle sounds (Dudzinski et al. 2009; Janik 2009). Recent research indicates that these are not discrete sounds, but rather that they occur along a continuum (Murray et al. 1998). At one end of this continuum are slow trains of clicks, in the middle are closely spaced clicks that sound like buzzes or squawks, and at the other end of the continuum are continuous sinusoidal waves (i.e., whistles). We still understand relatively little about functions of different categories of signals. However, studies suggest that click

trains are often used to explore the environment (e.g., Muller et al. 2008; Verfu*B* et al. 2009), click trains that turn into burst pulses are often used to localize prey just before a capture attempt (e.g., Koschinski et al. 2008; DeRuiter et al. 2009), and burst pulses and whistles are often used for communication (e.g., Janik 2000b; Foote et al. 2008).

Non-acoustic communication, which I do not investigate in this dissertation, also occurs during foraging. Non-acoustic communication includes body or tail slaps against the water (e.g., via noisy or somersaulting leaps), tilts of the body (likely facilitated by distinctive coloration patterns, Würsig et al. 1990), bubble emissions (Trudelle 2010), pectoral fin movements, and touching (Dudzinski 1998). A number of these behaviors at times appear to function in containing prey, but they likely have multiple purposes. For example, noisy leaps at the periphery of a prey ball may function in preventing fish from moving off sideways (Würsig 1986). At the same time, this percussive sound may call or attract other individuals to the feeding bout (similar to Janik 2000a).

Dusky dolphin foraging

Dusky dolphins are a good model to use to study foraging behaviors and functions of acoustic signals for several reasons. First, they often feed in a stationary manner, which allows one to study their behaviors not just above-water, but also underwater. Second, they are consistently found in several near-shore locations, which make it possible to study their behaviors for extended periods. Third, they exhibit complex coordination during foraging (Würsig and Würsig 1980; Vaughn et al. 2010a), which facilitates studying mechanisms of coordinated foraging.

Dusky dolphin foraging behaviors have been studied in some detail in 3 habitats: off Kaikoura, New Zealand (NZ), in the Marlborough Sounds, NZ, and in Golfo Nuevo and Golfo San José, Argentina (see Dahood and Benoit-Bird 2010; Vaughn et al. 2010a for summaries). Dusky dolphins have also been studied to a small extent off other regions of South America and NZ, and also off the west coast of South Africa. These studies indicate that dusky dolphins exhibit 2 broad foraging tactics: feeding at night on a deep scattering layer (e.g., off Kaikoura, NZ), and feeding during day on schools of small fishes. They feed via the latter tactic in the shallow bays of Admiralty Bay and Current Basin, NZ (located in the Marlborough Sounds), and Golfo Nuevo and Golfo San José, Argentina.

In this dissertation, I compare underwater foraging behaviors and acoustic signals between these 2 shallow bay habitats. Broad similarities combined with fine-scale differences make these 2 study locations ideal for a comparison of how ecology and social learning influence foraging behaviors and how acoustic signals are used during foraging. Additionally, dolphins at these 2 study locations have been separated for over one-half million years (Harlin-Cognato et al. 2007), which makes it possible to study potential long-term social learning differences between the locations.

Admiralty Bay and Current Basin, NZ

Admiralty Bay is a small bay of only about 160 km^2; adjacent Current Basin is about 30 km^2. As many as 220 dusky dolphins are found in these bays at any one time during winter and early spring (Markowitz et al. 2004), although a fair amount of dolphin turnover occurs. Despite turnover, this area is an important foraging habitat for

these dolphins, and 55% of individuals return here in consecutive winters (Markowitz et al. 2004). During feeding, group sizes are typically small (mean = 8 dolphins ± 5 SD), as are prey ball sizes (mean = 8m^2 ± 6 SD), and feeding durations are brief (mean = 5 min ± 6 SD) (Vaughn et al. 2007). Dusky dolphins here exhibit diverse feeding behaviors, and they feed both at depth and at the surface (Vaughn et al. 2008). Coordination is frequently evident, for example synchronized burst swims, leaps, and surfacing often occur. Occasionally feeding bouts become stationary, and at these times it is possible to observe herding and prey capturing behaviors underwater for these dolphins.

Golfo Nuevo and Golfo San José, Argentina

Golfo San José is approximately 4 times larger than Admiralty Bay, and Golfo Nuevo is about 16 times larger than Admiralty Bay; Current Basin is one-fifth the size of Admiralty Bay. These Argentina bays therefore probably contain more fish and dolphins than Admiralty Bay and Current Basin, NZ. This larger area may thus account for the larger schools of fish that appear to occur off Argentina, and the larger parties of dolphins that gather to contain and feed on those fish (Würsig and Würsig 1980).

Dusky dolphins have been studied since the 1970's in these Argentine bays (but at various times), and changes in the foraging behaviors of these dolphins, as well as in the ecology of the bays, have occurred during the past 40 years. During the 1970's, dusky dolphins here coordinated behaviors to herd large schools of fish towards the surface, and at times they fed for hours on these schools (Würsig and Würsig 1980). However, during the 1980's, a large number of these dolphins were caught and killed as

fisheries bycatch (Dans et al. 2003a); and during the 1990's, a fair number of anchovies were caught in fisheries (Dans et al. 2003b). Present-day foraging behaviors of dusky dolphins appear to be different from the 1970's, and these temporal differences may be due to these fishery-related or other human impacts, or due to natural changes in ecology. Today there appear to be fewer dusky dolphins in these bays, they feed on smaller schools of fish, and for shorter durations.

Research objectives

The purpose of my dissertation is to investigate ecological versus social learning influences on coordinated foraging behaviors, and how acoustic signals are used, by comparing 2 distinct dusky dolphin populations: Admiralty Bay and Current Basin, NZ and Golfo Nuevo and Golfo San José, Argentina. The overall question that I ask is "What behaviors do dolphins use to contain and capture prey, and how do these behaviors relate to differences in prey ball and group sizes in 2 distinct populations?" To answer this question, I analyze underwater video footage that was recorded during stationary feeding bouts. I describe and quantify prey herding and capturing behaviors, then relate these group behaviors to acoustic signals.

My specific research objectives were to:

1) Investigate how dusky dolphins coordinate behaviors to contain and capture schooling fishes under differing ecological conditions and in 2 distinct populations.
2) Describe categories of acoustic signals used by dusky dolphins.
3) Investigate proximate functions of signals during feeding.

Overview of chapters

I investigate coordination during foraging by quantifying behaviors that occur within 2 m of the prey ball, and acoustic signals. In Chapters II and III, I investigate behaviors, and in Chapters IV and V, I examine acoustic signals. All four of these chapters are written such that they can be submitted for publication in a journal.

In Chapter II, I describe dolphin underwater bait-balling behaviors, and examine how variations in behavior relate to group sizes, prey ball sizes, and location (Argentina compared to NZ). I focus on behaviors that occur within 2 m of the prey ball, including herding passes by the prey ball and prey-capture attempts. I also describe types of coordination that occur during these herding and prey-capture behaviors.

In Chapter III, I relate dolphin underwater bait-balling behaviors to prey ball escape behaviors off NZ to examine tactics used to contain prey balls and apparent costs and benefits of those tactics. I focus on changes in dolphin prey herding and capturing behaviors that occur when prey balls rapidly descend or ascend, or when they form funneling shapes that often precede rapid descending movements.

In Chapter IV, I describe categories of dusky dolphin acoustic signals, and examine similarities and differences between Argentina and NZ. I quantify inter-click intervals and duty cycles, then use these objective parameters to categorize signals for each location.

In Chapter V, I examine proximate functions of acoustic signals during bait-balling off NZ by relating signal parameters to behavioral parameters. I relate numbers of each signal category to numbers of behaviors per foraging interval.

Data sources

Video footage that I recorded in Admiralty Bay and Current Basin during 2005-2006 was used for underwater analyses off NZ, and footage recorded by the National Geographic Society during 1997-1998 in Golfo Nuevo was used for Argentine analyses. NZ acoustics data are from 2 sources. I used broadband recordings that were recorded by M Lammers off Kaikoura, NZ to determine what percentage of broadband (0-200 kHz) signals occurred at narrowband (0-16 kHz) frequencies. I then used narrow band recordings that were extracted from Admiralty Bay and Current Basin video footage to examine signal categories and functions. Argentine acoustics data were recorded by K Dudzinski during 1998. These data were recorded by a mobile video and acoustic system with 2 omni-directional hydrophones (Dudzinski et al. 1995).

Importance of research

There have been few studies of underwater dolphin foraging behaviors, and how acoustic signals are used in this context. One reason for this is because it is difficult to observe these behaviors underwater due to the mobile nature of dolphin feeding, limited water visibility, and the inaccessibility or unpredictability of many dolphin populations. The video footage and concurrent acoustics recordings of dusky dolphins off NZ and Argentina are thus unique and fortuitous. They provide an opportunity to describe underwater bait-balling behaviors and acoustic signals, and to ask specific questions of how ecology and social learning relate to these variables.

By increasing understanding of how ecology relates to dusky dolphin foraging behaviors, we are better able to predict how changes in ecology such as those due to

fisheries impacts may affect dolphins' ability to forage effectively. This information allows us to make better management decisions regarding fisheries, ecotourism, protected areas, and noise. Although I focus on dusky dolphin coordinated feeding behaviors in this dissertation, at least 15 of 33 delphinids at times coordinate behaviors to herd prey, many using tactics that are similar to those used by dusky dolphins (see Wells et al. 1999; Connor 2000; Heithaus and Dill 2009 for summaries). Since it is difficult to study foraging in detail for many of these delphinids, increasing our understanding of dusky herding and prey-capture behaviors is useful in helping us learn more about behaviors of dolphins that forage in a similar manner, which likewise has conservation value.

Finally, increasing our understanding of types of coordination that occur during foraging and how acoustic signals facilitate this coordination deepens our appreciation of dolphin societies. Conservation is facilitated by an appreciation and love of nature, and increasing our understanding of behavioral diversity that occurs in marine environments is one way to increase our appreciation of these ecosystems. This is the case not just within the scientific community, but also for the general public. My dissertation is written in a format such that each chapter is publishable as a manuscript in a scientific journal. However, I also plan to share this information with the public through a combination of presentations, nature writing, photography, and video montages. My goal is for these media to connect people more closely with the marine environment. My hope is that this increased empathy in turn leads to increased respect and love for marine environments, and conservation action.

CHAPTER II

DOLPHIN UNDERWATER BAIT-BALLING BEHAVIORS IN RELATION TO GROUP AND PREY BALL SIZES

Introduction

Predator-prey interactions involve behaviors that predators use to feed on prey, and behaviors that prey use to avoid being eaten. From a predator's viewpoint, foraging includes the stages of locating, containing, capturing, and consuming prey. The costs and benefits of engaging in these behaviors individually versus in different-sized groups depend on the ecological context that includes prey parameters, predator parameters, and other factors (Krebs and Davies 1993; Hoare et al. 2004; Gowans et al. 2008). Examples of prey parameters that can affect costs and benefits of foraging behaviors for the predator include distribution of prey, sizes or elusiveness of patches, and energetic content of different prey species. Predator parameters that can affect foraging costs and benefits for the predator include group size, sensory capabilities, hunting tactics, familiarity or association-frequency between group members (i.e., that can affect how well group members work together), or intra-specific interactions with other groups in the area. Additional factors affecting foraging costs and benefits include the potential risk of a predator becoming prey, or inter-specific competition.

Dolphins and other predators frequently coordinate behaviors during foraging, which can make it less costly to locate or contain prey. In-depth characterization of these behaviors is key to understanding the relationship between behavioral costs and

benefits and in turn how foraging success influences foraging decisions. When locating prey, individuals often coordinate searching behaviors by remaining in acoustic contact as they spread out in line or other formations (Heithaus and Dill 2009); these formations allow predators to search a larger area. Individuals coordinate behaviors to contain prey by diverse tactics including corralling it between subgroups (e.g., Boesch and Boesch 1989; Burgess 2006), or spreading out to drive prey toward a barrier (e.g., Hoese 1971; Similä and Ugarte 1993).

Coordinating behaviors during prey-capture attempts can also make it easier for individual predators within a group to capture prey. Coordinated prey captures can make it easier for a dolphin to capture a fish when the group works together to isolate individual fish or a small number of fish from a school, which reduces the "confusion effect" (Norris and Schilt 1988), and thereby makes it easier for a dolphin to focus on a single fish (e.g., Similä and Ugarte 1993; Fertl and Würsig 1995). Coordinating behaviors while capturing prey can also make it easier for a dolphin to capture a fish by causing a school's behaviors to become more disrupted than they would if fewer predators were present (similar to Wilson et al. 1987). Finally, coordinated prey-capture attempts can reduce prey escape options if dolphins trap fish between themselves just prior to prey capture (e.g., bottlenose dolphins off Florida, Gazda et al. 2005).

Behavioral comparisons between distinct populations of a single species provide insights into how ecology relates to behaviors by broadening the range of ecological conditions across which we can examine relationships, and by allowing us to separate relative influences of ecology versus social learning. For example, inter-population (and

inter-species) similarities in how ecological context relates to grouping patterns or other behaviors provide insights into behavioral costs and benefits (Lusseau et al. 2004; Gowans et al. 2008; Benoit-Bird et al. 2009). On the other hand, group or population specific behaviors that are not accounted for by ecological variations suggest that social learning may play a role (Rendell and Whitehead 2001).

Dusky dolphins are semi pelagic delphinids that resides in the southern hemisphere, mainly off South America, NZ, and southwestern Africa (Würsig et al. 2007). They feed using 2 generalized tactics that are habitat-specific. In areas where there is a deep scattering layer (e.g., off Kaikoura, NZ), they feed at night, when this layer is closest to the surface (Dahood and Benoit-Bird 2010). Over a continental shelf (e.g., in the Marlborough Sounds, NZ and in Argentina), they feed during daytime on schooling fishes (mainly small fishes of the Order Clupeiformes such as pilchard, *Sardinops neopilchardus*, and anchovies; Vaughn et al. 2010a). During stationary feeding bouts, water clarity permits underwater observation of bait-balling behaviors (e.g., Vaughn et al. 2007).

Comparing underwater foraging behaviors between Argentina and NZ dusky dolphin populations provides a unique opportunity for increasing our understanding of the costs and benefits of coordinated foraging in relation to prey ball and dolphin group size. In both locations, dusky dolphins coordinate behaviors to herd and capture schooling fish, and they feed with a diverse multi-species assemblage that includes seabirds, pinnipeds, and sharks (Vaughn et al. 2010a). However, in Argentina, dusky dolphins feed in much larger groups (up to 300 dolphins compared to a range of just 1–

30 dolphins in Admiralty Bay and Current Basin, NZ; Würsig and Würsig 1980, Vaughn et al. 2007) and for longer durations (up to 3 h compared to a range of just 1–42 min in Admiralty Bay and Current Basin, NZ; Würsig and Würsig 1980; Vaughn et al. 2007). These differences likely relate to differences in prey ball sizes. Prey balls may be larger in Argentina due to differences in sizes of bays (Vaughn et al. 2010a). Admiralty Bay and Current Basin, NZ are only 30 km^2 and 160 km^2, respectively, while Golfo Nuevo and Golfo San Josè, Argentina (where dusky dolphin foraging has been studied intensively; Würsig & Würsig 1980; Degrati et al. 2008) are 2500 km^2 and 750 km^2, respectively.

My objectives were to characterize dusky dolphin prey herding and capture behaviors observed underwater in Argentina and NZ, and to investigate how these behaviors related to prey ball size, dolphin group size, and location. I described and quantified behaviors from video footage that was recorded in Admiralty Bay and Current Basin, NZ, and Golfo Nuevo, Argentina.

Methods

Study locations

Video footage was analyzed from Admiralty Bay (40°57'S, 173°55'E) and Current Basin (40°57'S, 173°48'E), NZ and Golfo Nuevo (42°40'S, 64°40W), Argentina. Admiralty Bay and Current Basin are located in the Marlborough Sounds region at the northern part of the south island of NZ, where they are connected by French Pass. Golfo Nuevo is located in the northern part of the coastal Patagonia region of Argentina. All three bays are somewhat shallow in depth. Admiralty Bay and Current

Basin have typical depths of 30-50 m and 20-30 m, respectively; Golfo Nuevo has a typical depth of 40-100 m. Water clarity in Admiralty Bay and Current Basin during the 2005 and 2006 study seasons was a mean of 10 m ± 3 SD (range = 5-18 m measured using a Secchi disk, Vaughn et al. 2010b). Water clarity was not measured in Golfo Nuevo during the present study.

Data collection

In NZ, data were recorded from 5 August to 4 November 2005 and during August 2006, using a rigid-hulled inflatable boat with an 85 hp 2-stroke (2005) or an 80 hp 4-stroke (2006) Yamaha engine. Data were collected only when Beaufort sea states were ≤ 3. To locate dolphin groups, we drove on predetermined transects. A group focal follow was then conducted for up to 4 h, and above-water data were recorded at 2-min intervals. Above-water data included group size and predominant behavior. Group size was considered to include all dolphins that were ≤ 10 m from another dolphin (Smolker et al. 1992). Predominant behavior was that exhibited by most of the dolphins for most of the 2-min interval. My definition of 'feeding' behavior was "high-level activity that changed direction often and that included leaps or burst swims". One observer recorded above-water dolphin data, at a distance of 25-50 m from the group. During stationary feeding, one observer recorded underwater video footage via surface swimming and shallow breath-hold diving, at a distance of 5-8 m from the prey ball. Underwater video was recorded using a Sony DCR-HC1000 video camera in an Amphibico housing. Video times were synchronized with above-water follow data by recording focal follow interval times to the second.

To examine Argentina behaviors, I analyzed underwater video footage that was recorded in Golfo Nuevo during December of 1997 and 1998. Footage was recorded by a SCUBA diver using a handheld video camera. The only exception was footage from one feeding bout, which was recorded using a remote camera that was connected to the side of the vessel.

Underwater behavioral quantification

NZ video data were organized according to visibility of the prey ball and nearby dolphin behaviors. I analyzed herding and prey-capture behaviors for those prey balls for which I could see the entire prey ball (except the back side), and all dolphin behaviors within 2 m of the prey ball, for at least 1-min during a focal follow. Additionally, I analyzed prey-capture behaviors for prey balls for which I could see the entire prey ball (except the back side), and all dolphin behaviors adjacent to the prey ball, for at least 1 min during a focal follow.

From Argentina video data, I analyzed all herding and prey-capture behaviors for all feeding bouts. However, for larger prey balls, it was usually only possible to see a small proportion of herding passes or prey-capture attempts, since only a portion of these prey balls were in the field of view of the video camera. For smaller prey balls, even though I could often see the entire prey ball, it was not possible to quantify behaviors for continuous 1-min intervals, because these prey balls frequently moved in and out of view. Thus, for Argentine behaviors, I analyzed data at the level of individual behaviors, but I was not able to determine numbers of behaviors per unit time.

For both locations, I conducted individual focal follows on all dolphins that swam within 2 m of a prey ball, using the mean length of an adult dusky dolphin (approximately 2 m; Cipriano 1992; Koen-Alonso et al. 1998) as a size reference to estimate distance. A "herding pass" was defined as the duration of time during which a dolphin was within 2 m of the prey ball. A "prey-capture attempt" was indicated by a dolphin swimming adjacent to a prey ball while exhibiting a slight burst of speed towards the prey ball, a head tilt towards the prey ball, or a slight spray of fish away from the dolphin. A single herding pass could include no or multiple prey-capture attempts.

For each herding pass, I recorded if dolphins swam closest to the top, side, or bottom of the prey ball. The top and bottom of the prey ball was defined as one-third of the two dimensional surface that was most near to or far from the surface of the water. I also recorded if dolphins swam clockwise or counterclockwise around the prey ball during the herding pass, with respect to the surface. A herding pass was categorized as "clockwise" or "counterclockwise"; it was categorized as "other" if there was no directionality (e.g., if the dolphin swam under, over, or through the prey ball), or if the dolphin swam both clockwise and counterclockwise during a herding pass. For each complete herding pass that did not include a prey-capture attempt, I recorded what region of the dolphin (dorsal, side, or ventral) faced the prey ball when the dolphin was closest to the prey ball.

For each prey-capture attempt, I recorded location (Figure 2 top), and number of other dolphins within 2 m of the prey ball (i.e., subgroup size). For attempts that

occurred on the side of the prey ball, body orientation was recorded according to what region of the dolphin (dorsal, side, or ventral) faced the prey ball at the time of the attempt.

I quantified degree of coordination between individuals similar to Boesch and Boesch (1989), according to temporal and spatial synchronicity between individuals doing prey-capture attempts and complementary behaviors (Figure 2 bottom). A low level of coordination was defined as attempts that were synchronized temporally (occurred within one second of each other) but not spatially. A medium level of coordination was defined as attempts that were synchronized temporally and spatially (occurred within 2 m of each other), but that did not involve complementary behaviors. A high level of coordination was defined as attempts that were synchronized temporally and spatially that involved complementary behaviors (i.e., converging, crisscrossing, or pinwheel formation). Complementary behaviors were defined as those in which prey was trapped between dolphins.

For each feeding bout, I measured the 2-dimensional area of prey balls with Image J (http://rsb.info.nih.gov/ij/), using the mean length of an adult dusky dolphin as a reference (NZ: 1.73 m, *sensu* Cipriano 1992; Argentina: 1.66 m, *sensu* Koen-Alonso et al. 1998). The size of the entire prey ball was measured when possible. For Argentina, when it was not possible to measure the entire prey ball, size was recorded as a minimum. For each 2-min interval during a feeding bout, I recorded if fish in the prey ball were swimming in a clockwise, counterclockwise, or other direction, with respect to the surface.

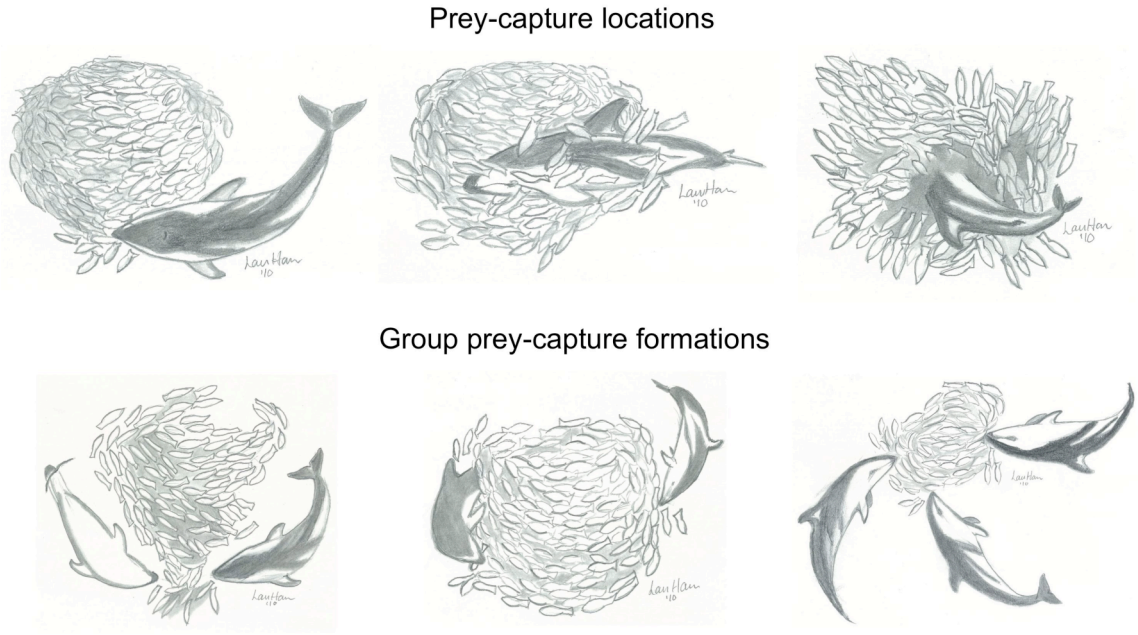

Figure 2. Illustrations showing locations of individual prey-capture attempts and complementary formations. Illustrations in top row show examples of individual prey-capture attempts that occur on the side of the prey ball (left), through the edge of the prey ball (center; dolphin visible through fish spray), and through the prey ball (right; dolphin not visible through fish). Illustrations in bottom row show complementary formations observed during dolphin prey-capture attempts: converging (left; dolphins swim towards each other), crisscrossing (center; dolphins swim around prey ball in opposite directions and attempt to capture prey on opposite sides of prey ball), and pinwheel (right; dolphins swim around prey ball in same direction and attempt to capture prey on opposite sides of prey ball) formations. Illustrations by Lauren Hansen.

Behavioral analyses

A feeding bout was defined as a discrete period of feeding based on consecutive 2-min above-water intervals for which dolphin behavior was categorized as feeding. Median dolphin group sizes in NZ were calculated for each 2-min feeding interval using the number of dolphins present at the start and end of an interval (see below for why we used medians). Dolphin group sizes in Argentina were not recorded in this study.

I summarized herding and prey-capture parameters separately for the NZ and Argentina datasets. For both datasets, I examined individual behaviors and calculated percentages of those behaviors for each feeding bout. For Argentine data regarding location of herding passes, the data were quantified only from those prey balls for which the top, bottom, and sides of the prey balls were equally visible across the entire feeding bout. For the NZ dataset, I also calculated numbers of behaviors per 1-min and the timing between behaviors. I summarized numbers of underwater behaviors per 1-min because I frequently was not able to reliably quantify underwater behaviors for a longer duration. One-minute underwater intervals occurred within 2-min above water intervals. Prey ball sizes were categorized as small (< 6 m^2), large (6-18 m^2), or very large (> 18 m^2).

Statistical analyses

SPSS version 13.0 for Mac OS X software (SPSS Inc., Chicago, IL) was used for statistical analyses. Non-parametric statistics were used to analyze data because of small sample sizes and non-normal distributions. I used Chi-square (CS) and Mann-Whitney U (MW) tests, and Spearman Rank Order correlations (SR) to examine relationships between variables. The type of test used depended on whether variables were categorical or continuous. Feeding bouts were considered independent, because they occurred on different prey balls at different times. Median values per feeding bout were used as our statistical unit of analysis (e.g., median proportion of herding passes that occurred on the top versus side versus bottom of the prey ball). I used a 2-tailed alpha

level of 0.05 for all analyses. Descriptive statistics are presented as medians ± inter-quartile ranges (IQR).

Results

Individual focal follows

From the NZ video I quantified herding behaviors while doing 2,460 individual focal follows from 70 1-min intervals during 19 feeding bouts. I quantified prey-capture behaviors from 89 1-min intervals during 21 feeding bouts. Median duration of NZ individual focal follows was 3.8 s (IQR = 2.5-5.4, range = 0.2-27.7, N = 2,460). From Argentine video, I observed dolphins in the vicinity of 23 prey balls. However, a dolphin only swam within 2 m of 21 of those prey balls, and a dolphin only attempted to capture prey from 15 of those prey balls. I conducted 575 individual focal follows in Argentina, with a resulting median duration of 2.7 s (IQR = 1.6-5.1, range = 0-32.8, N = 575).

Dolphin group and prey ball sizes

In NZ, dolphin group and prey ball sizes were small. Across the underwater dataset, group size was a median of 12 dolphins (IQR = 7-17, range = 4-20, N = 21). Median prey ball size in NZ was 5 m^2 (IQR = 3-10, range = 1-18, N = 52). In Argentina, I observed the entire prey ball in the video field of view for 11 of 23 prey balls, while I observed only part of the prey ball for 12 of 23 prey balls. For the former 11 prey balls, median size was 2 m^2 (IQR = 1-6, range = 0.1-22, N = 11). All of the latter 12 prey balls were > 7 m^2.

I observed larger prey balls in Argentina than in NZ (Figure 3). In Argentina, 65% of prey balls were large (6-18 m^2) or very large (> 18 m^2), compared to only 52% of prey balls in NZ. The largest prey ball documented in NZ was 33 m^2. In Argentina, at least six prey balls were > 36 m^2 with the largest prey ball at > 74 m^2. Argentina dolphins attempted prey captures on 3 of these very large prey balls; the sizes of these prey balls were > 37 m^2 (2 prey balls) and > 74 m^2. These sizes were minimum areas and likely underestimated, since I could only see a portion of the prey balls in the video field of view. For example, for the latter three prey balls, I estimated that I could see about 30%, 30%, and 60% of each prey ball, based on curvature of each ball.

Prey balls on which dolphins attempted prey-captures were also larger in Argentina than in NZ (Figure 3). For prey balls on which dolphins attempted at least one prey-capture, location was related to ball size (CS test: $X^2 = 16.136$, $P < 0.001$). A similar proportion of these prey balls were small in Argentina (47%) compared to NZ (48%) ($X^2 = 0.009$, $P = 0.923$); however, a greater proportion of prey balls were large in NZ (48%) than in Argentina (13%) ($X^2 = 8.531$, $P = 0.014$), while a greater proportion of prey balls were very large in Argentina (40%) than in NZ (4%) ($X^2 = 14.608$, $P = 0.001$) (CS tests).

In Argentina, when dolphins were in the vicinity of a small prey ball, they almost always attempted at least one prey capture (7 of 8 small prey balls). In contrast, when they were in the vicinity of large or very large prey balls, they only attempted a prey capture on 8 of 15 prey balls. Prey ball size was not statistically related to whether or

not at least one prey-capture attempt was observed for dolphins that were in the vicinity of a prey ball (CS test: $X^2 = 2.685$, $P = 0.101$).

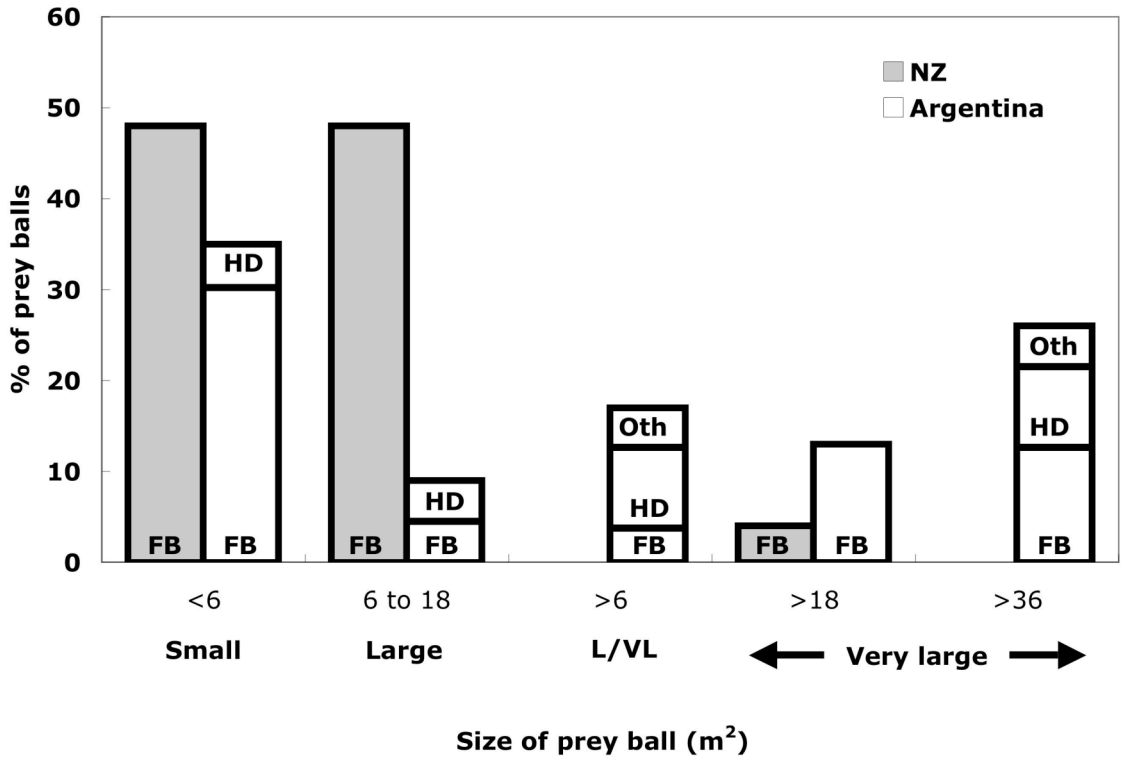

Figure 3. Percentages of small, large, and very large prey balls observed in NZ and Argentina. We observed 52 prey balls in NZ and 23 prey balls in Argentina. "FB" indicates feeding bouts, or those prey balls for which we observed a dolphin attempting a prey-capture. "HD" indicates herding, or those prey balls for which a dolphin swam within 2 m of the prey ball but did not attempt to capture prey. "Oth" indicates other prey balls for which dolphins were present but did not swim within 2 m.

Herding passes: similarities and differences between locations

In NZ, there was a median of 3 herding passes per 1-min interval per dolphin (IQR = 2-5, range = 0.4-8, $N = 68$). Duration of complete herding passes and the

proportion that included a prey-capture attempt were similar between locations. Median duration of complete herding passes was 2.3 s in NZ (IQR = 1.6-3.3, range = 0.4-13.3, *N* = 399), and 2.4 s in Argentina (IQR = 1.8-3.0, range = 0.90-13.6, *N* = 45). In NZ, 36% of complete herding passes included a prey-capture attempt, and these passes typically included just one prey-capture attempt. Three passes included two prey-capture attempts, and one pass included three prey-capture attempts. In Argentina, 38% of complete herding passes included a prey-capture attempt, and these passes also typically included just one attempt. However, one pass included two attempts.

When engaged in herding passes, dolphins typically circled the prey ball in a clockwise direction (NZ: 95% = clockwise, 2% = counterclockwise, 3% = other, *N* = 2,753; Argentina: 57% = clockwise, 7% = counterclockwise, 36% = other, *N* = 586). When dolphins swam in a direction other than clockwise or counterclockwise, they most often swam under the prey ball (NZ: 36% of other herding passes; Argentina: 74% of other herding passes). In NZ, prey balls typically rotated in a clockwise direction (10 of 15 prey balls). Prey balls that rotated in a clockwise direction were more often small prey balls, while prey balls that did not rotate in a clockwise direction were more often large prey balls. Small prey balls in Argentina also typically rotated in a clockwise direction (5 of 8 prey balls).

There were differences between study locations with respect to locations of herding passes. In NZ, 55% of herding passes occurred on the side of the prey ball, while 34% occurred on the bottom and 11% occurred on the top (*N* = 2,753). In Argentina, 47% of herding passes occurred on the side of the prey ball, while 48%

occurred on the bottom and 5% occurred on the top ($N = 279$). For small prey balls, location was related to the proportion of herding passes that occurred on the top ($Z = -2.109$, $P = 0.035$) of prey balls, but it was not related to the proportion that occurred on the bottom ($Z = -1.854$, $P = 0.070$) or side ($Z = -1.562$, $P = 0.133$) (MW tests; Figure 4). I summarized data on locations of herding passes only for those feeding bouts for which I could quantify location for at least 10 passes.

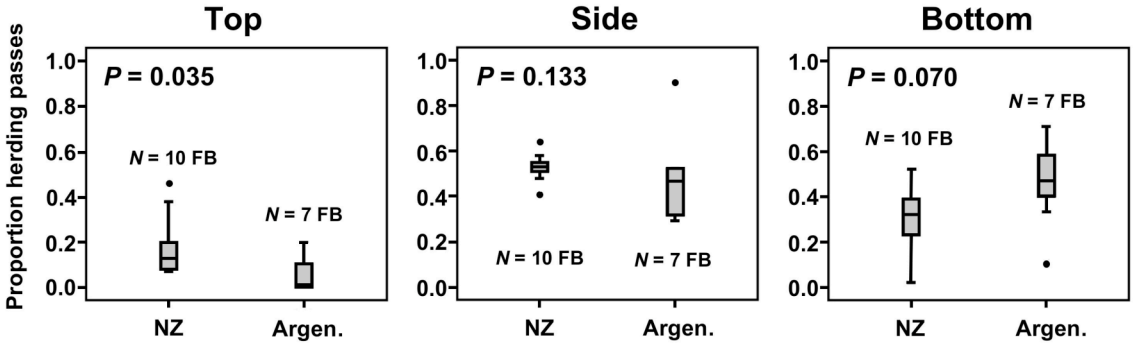

Figure 4. For small prey balls, proportion of herding passes that were on the top, side, and bottom of prey balls, for each study site.

There were also differences between study locations in body orientation for complete herding passes during which a prey-capture attempt did not occur. In NZ, dolphins had a side orientation for 60%, a ventral orientation for 24%, and a dorsal orientation for 16% of these passes ($N = 255$). In Argentina, dolphins had a side orientation for 45%, a dorsal orientation for 34%, and a ventral orientation for 21% of these passes ($N = 28$).

Herding pass parameters in relation to dolphin group and prey ball sizes

In NZ, as dolphin group size increased, a greater proportion of herding passes occurred on the bottom of the prey ball ($P < 0.001$) and a smaller proportion of herding passes occurred on the top of the prey ball ($P < 0.001$); group size did not relate to proportion of passes on the side of the prey ball ($P = 0.146$) (SR correlations; Figure 5a). Group size was not related to number of herding passes per dolphin per interval ($P = 0.194$), the proportion that included a prey-capture attempt ($P = 0.475$), or duration ($P = 0.879$) (SR correlations).

In NZ, prey ball size did not relate to the number of herding passes per dolphin per interval (MW test: $Z = -1.866$, $P = 0.062$), although more herding passes occurred per dolphin per interval when dolphins were feeding on small prey balls than when they fed on large prey balls (Figure 6a). Prey ball size also did not relate to location of passes (top: $Z = -0.178$, $P = 0.859$; side: $Z = -0.489$, $P = 0.625$; bottom: $Z = -0.044$, $P = 0.965$), the proportion that included a prey-capture attempt ($Z = -0.623$, $P = 0.533$), or duration ($Z = -0.647$, $P = 0.518$) (MW tests). For analyses of duration of complete herding passes, we only included those feeding bouts during which at least 10 complete herding passes occurred.

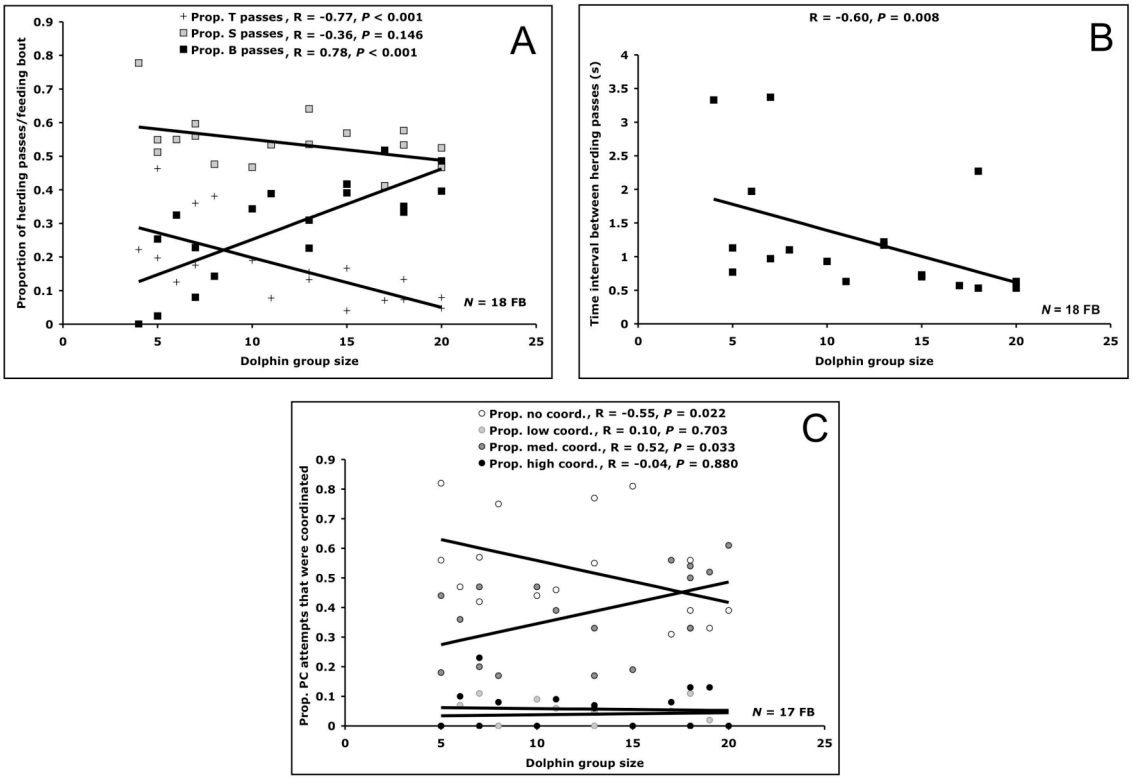

Figure 5. Median dolphin group size in NZ in relation to proportion of herding passes per feeding bout that occurred on the top (T), side (S), and bottom (B) third of prey balls (A), duration between the start of subsequent herding passes (B), number of prey-capture attempts per 1-min feeding interval (C), and proportion of prey-capture attempts (PC) for which dolphins used no or a low, medium, or high degree of coordination (D). Lines show linear trends. FB = feeding bouts.

Prey-capture attempts: similarities and differences between locations

In NZ, there was a median of 0.9 attempts per dolphin per 1-min interval (IQR = 0.5-1.5, range = 0-4.5, $N = 85$). Location of attempts and body orientations differed between locations. In NZ, 83% of attempts occurred on the side, 13% occurred through the edge, and 4% occurred through the prey ball ($N = 1{,}017$). In Argentina, 69% of attempts occurred on the side, 23% occurred through the edge, and 8% occurred through

the prey ball ($N = 242$). When attempting a prey capture on the side of the prey ball, in NZ, dolphins had a ventral orientation for 83%, a side orientation for 15%, and a dorsal orientation for 2% of attempts. In Argentina, dolphins had a ventral orientation for 82%, a side orientation for 12%, and a dorsal orientation for 6% of attempts.

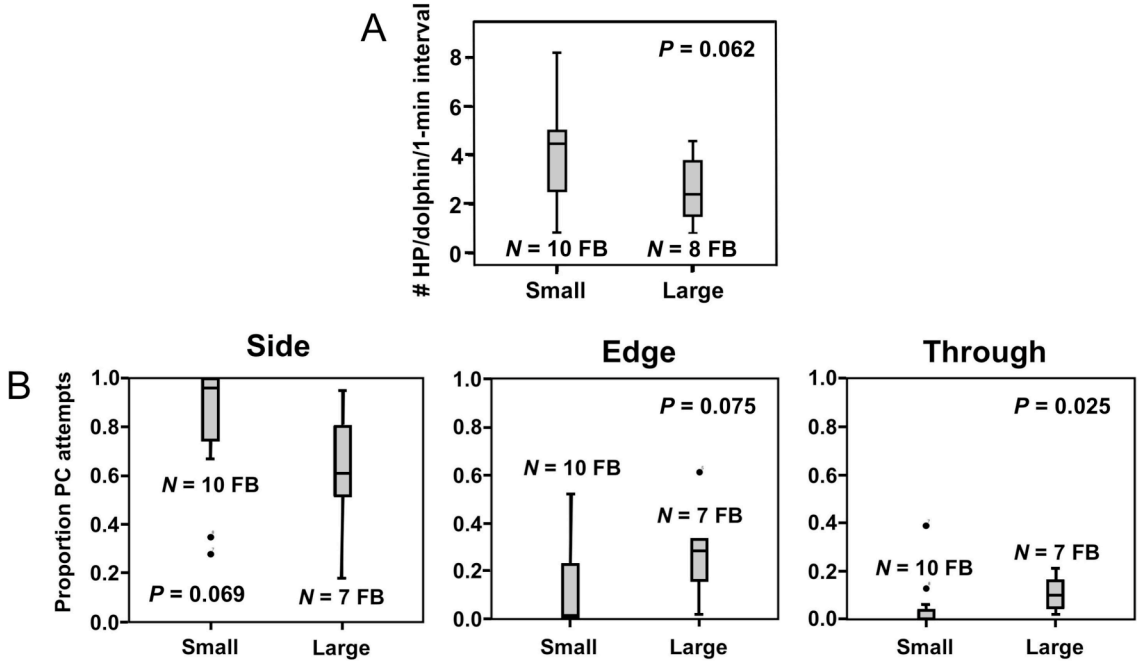

Figure 6. Differences between small (< 6 m^2) and large prey balls (≥ 6 m^2) in NZ. Part A shows differences in number of herding passes per dolphin per 1-min interval. Part B shows proportion of prey-capture attempts that occurred on the side, through the edge, or through the prey ball. For part B, we only included those feeding bouts for which at least 10 prey-capture attempts occurred. PC = prey capture. FB = feeding bout. HP = herding passes.

A unique individual prey-capture behavior that infrequently occurred was "somersaulting". This behavior was defined as the dolphin doing at least a 90° end-over-end rapid rotation as it attempted a prey capture. I only observed this behavior

once in NZ, early in a feeding bout, when a fairly large group of 18 dolphins were feeding on a small prey ball (3 m^2). In Argentina, I observed this behavior often (N = 14) during a single feeding bout that was recorded with the remote camera. This prey ball was small (7 m^2), loosely packed, and very mobile (i.e., the prey ball was glimpsed several times, but only briefly each time). Although it was not possible to determine the total number of dolphins that exhibited somersaulting prey-capture attempts, a minimum of 3 different dolphins exhibited this type of prey-capture behavior. During this feeding bout, I observed a maximum of 16 dolphins in a single video frame. It is likely that many of these dolphins did somersaulting prey-capture attempts, since only one attempt was documented that did not include somersaulting.

Prey-capture parameters in relation to dolphin group and prey ball sizes

In NZ, dolphin group size did not relate to number of attempts per dolphin per interval (P = 0.419, N = 20 feeding bouts) or location of attempts (side: P = 0.452; edge: P = 0.670; through: P = 0.569; N = 17 feeding bouts for which at least 10 attempts occurred) (SR correlations). Dolphin group size also was not statistically related to the proportion of ventral (P = 0.876), side (P = 0.729), or dorsal (P = 0.139) attempts (SR correlations; N = 19 feeding bouts), although individuals in larger groups had a greater proportion of attempts with a dorsal orientation (R^2 = 0.124).

In NZ, prey ball size was related to location of prey-capture attempts (side: Z = -1.820, P = 0.069; edge: Z = -1.782, P = 0.075; through: Z = -2.241, P = 0.025; MW tests; N = 17 feeding bouts for which at least 10 prey-capture attempts occurred; Figure 6b). However, prey ball size did not relate to number of attempts per dolphin per

interval (MW test: Z = -1.331, $P = 0.183$, $N = 20$). Prey ball size also did not relate to the proportion of ventral (Z = -1.408, $P = 0.159$), side (Z = -0.744, $P = 0.457$), or dorsal (Z = -1.092, $P = 0.275$) attempts (MW tests; $N = 19$ feeding bouts).

Coordination during herding and prey-capture behaviors

I quantified coordination by measuring timing and by comparing subgroup to individual behaviors. In NZ, most herding passes and prey-capture attempts occurred closely together in time (Figure 7). A total of 55% of herding passes occurred < 1 s, 77% of passes occurred < 2 s, and 94% occurred < 5 s after the previous pass. Median timing between herding passes was 0.8 s (IQR = 0.3-1.87, range = 0-33.9, $N = 2{,}753$). Timing of herding passes related to group size (SR correlation: $P = 0.008$, $N = 18$; Figure 5b), but it did not relate to prey ball size (MW test: Z = -0.934, $P = 0.350$, $N = 18$). A total of 31% of prey-capture attempts occurred < 1 s, 50% occurred < 2 s, and 76% occurred < 5 s after the previous attempt. Median timing between attempts was 2.0 s (IQR = 0.7-4.8, range = 0-73.8 s). Timing of attempts did not relate to group size (SR correlation: $P = 0.163$, $N = 17$ feeding bouts) or prey ball size (MW test: Z = -0.402, $P = 0.687$, $N = 17$ feeding bouts).

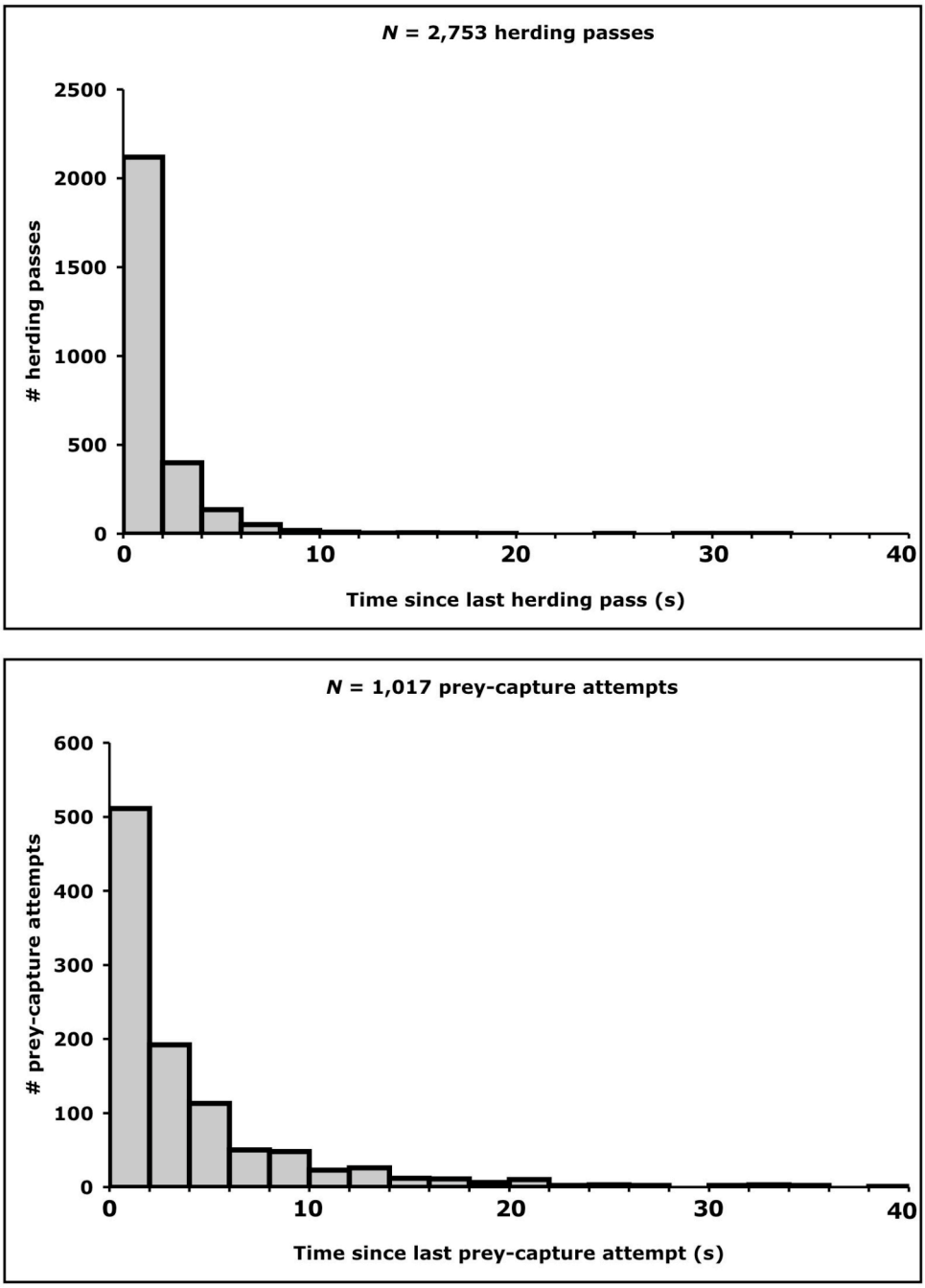

Figure 7. Time intervals between herding passes (top) and prey-capture attempts (bottom) in NZ. Timing of herding passes was measured as the duration between the start times of two consecutive herding passes, i.e., the time at which a dolphin is first within 2 m of a prey ball. One prey-capture attempt occurred > 40 s after the previous attempt.

In NZ, the majority of complete herding passes that did not include a prey-capture attempt were subgroup behaviors (85%, $N = 255$ passes). Median subgroup size was 3 dolphins (IQR = 2-4, range = 2-9, $N = 217$). Of the complete herding passes that occurred in subgroups, 39% included at least one other dolphin that attempted a prey capture within 1 s of the time of closest approach by the focal dolphin. When a dolphin approached within 2 m of a prey ball, whether or not the dolphin attempted to capture a fish did not relate to whether it was in a subgroup versus alone (MW test: Z = -1.544, $P = 0.123$, $N = 9$ feeding bouts for which there were 5 complete herding passes of each type). Subgroup size also did not appear to relate to whether or not the focal dolphin attempted a prey capture when it swam within 2 m of the prey ball (Figure 8).

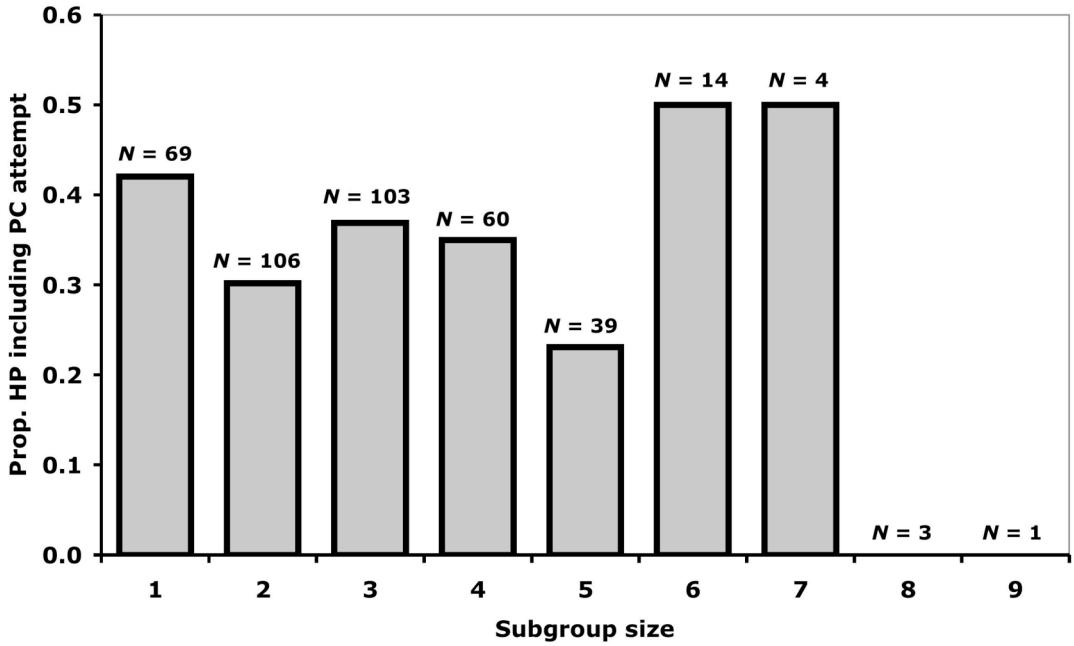

Figure 8. Subgroup sizes in relation to proportion of complete herding passes (HP) that included a prey-capture attempt (PC) in NZ. $N = 399$ complete herding passes.

In NZ, the majority of prey-capture attempts were subgroup behaviors (84%, N = 831). Median subgroup size was 3 dolphins (IQR = 2-4, range = 2-9). For attempts that occurred in a subgroup, 26% included at least one dolphin that was on the opposite side of the prey ball from the focal dolphin. In total, 51% of attempts were temporally synchronized, 47% were temporally and spatially synchronized, and 8% were complementary (N = 1,074). Complementary attempts most often occurred in a pinwheel formation (91%), although 5% occurred in a crisscrossing formation, and 4% occurred in a converging formation. In Argentina, the majority of prey-capture attempts also were subgroup behaviors (63%, N = 16). Median subgroup size was 2 dolphins (IQR = 2 dolphins, range = 2-4, N = 16). In total, 48% of attempts were temporally synchronized, 39% were temporally and spatially synchronized, and 10% were complementary (N = 62). Complementary attempts most often occurred in a converging formation (83%), while a crisscrossing formation was observed on one occasion.

In NZ, larger dolphin groups had a greater proportion of prey-capture attempts where a medium degree of coordination occurred (P = 0.033) and a smaller proportion of attempts where no coordination occurred (P = 0.022) (SR correlations; N = 17 feeding bouts for which there were ≥ 10 prey-capture attempts; Figure 5d). Dolphin group size was not related to proportion of attempts where a low (P = 0.703) or high (P = 0.880) degree of coordination occurred (SR correlations). Prey ball size was not related to proportion of attempts where no (Z = -0.151, P = 0.880), a low (Z = -0.266, P = 0.790), a medium (Z = -0.302, P = 0.763) or a high (Z = 0.531, P = 0.595) degree of coordination occurred (MW tests; N = 17 feeding bouts).

Discussion

Dolphin group and prey ball sizes

In Argentina, prey balls were larger and dolphins fed on larger prey balls, and this may be due to bay size or ecological differences between the bays. Golfo Nuevo, Argentina is much larger (2500 km^2) than Admiralty Bay and Current Basin, NZ (160 km^2 and 30 km^2, respectively), so it may provide habitat for larger fish schools. Fish school sizes may be smaller in NZ bays due to lower food abundance or predation risk, although these variables have not to my knowledge been quantified for these regions. Schooling fishes often congregate in large prey balls, but may split into smaller balls during daily migrations (Similä 1997), due to reduced food availability (Duffy and Wissel 1988); or they may be found in smaller groups when there is lower predation risk (Hoare et al. 2004).

Although dolphin group sizes in Argentina were not recorded during this study, an overlapping study during December, 1998 and January, 1999 recorded a maximum group size of 80-100 dolphins across 12 research days (K Dudzinski, unpublished data), which is much larger than the maximum group size of 20 dolphins recorded for this study in NZ. Previous studies have also found dolphin group sizes to generally be larger in Argentina than in NZ (Vaughn et al. 2010a). Group size differences between locations likely also related to differences in habitat sizes.

Dolphin herding and capture behaviors: similarities and differences between locations

Herding passes were most likely to occur on the side or bottom of prey balls at both locations. By preferentially swimming around the side or under prey balls,

dolphins likely facilitated movement of prey closer to the surface (Würsig and Würsig 1980; Nøttestad et al. 2002; Vaughn et al. 2008), or prevented prey from escaping horizontally or vertically (Similä and Ugarte 1993; Fertl and Würsig 1995). Dusky dolphins typically swam by the prey ball briefly when doing herding passes, and in a clockwise direction. Circling around prey balls in a clockwise direction may prevent dolphins from getting in each other's way, and it may also be indicative of a mammalian right-sided tendency. Similarly, gray (*Eschrichtius robustus*, Woodward and Winn 2006), fin (*Balaenoptera physalus*, de Guevara et al. 2008), and humpback (Clapham et al. 1995) whales have a right-sided tendency during feeding dives, and bottlenose dolphins show a right-sided tendency when strand feeding in South Carolina (Hoese 1971). These right-sided tendencies during feeding may relate to laterality in right vs. left brain functions (Karenina et al. 2010), or it may be due to feeding anatomy.

However, in Argentina a larger percentage of herding passes occurred on the bottom of a prey ball, and dolphins were less likely to swim clockwise and more likely to swim directly under prey balls than were dolphins in NZ. As a result, dolphin behaviors in Argentina would have been more likely to move prey balls to the surface. It is possible that dusky dolphins in Argentina focused more on herding prey balls to the surface, either because "good" prey balls were more difficult to locate (e.g., small prey balls, Krause and Godin 1995), or because the larger dolphin groups that were found there were better able to focus simultaneously on herding and capturing fish (Würsig 1986).

Only about one third of complete herding passes included a prey-capture attempt at both locations, which indicates that dusky dolphins used herding behaviors that were independent of prey-capture behaviors (as has been hypothesized for a number of delphinids, Vaughn et al. 2010a). During complete herding passes that did not include a prey-capture attempt, dolphins were most likely to have a side body orientation. Although a ventral body orientation may be effective in containing prey, a side orientation may be just as, or more, effective. Penguins from the genus *Spheniscus*, which have body coloration similar to dusky dolphin color patterns, most effectively disrupt schooling behaviors of fish when their sides face a prey ball (Wilson et al. 1987). This is because their sides have a conspicuous coloration, which may act as a high intensity visual stimulus to the fish (Wilson et al. 1987). Alternatively, the distinct black and white coloration on the sides of dusky dolphins may function in short-distance communication during foraging (Würsig et al. 1990).

At both study locations, herding passes and prey-capture attempts occurred closely together in time and space, and coordination frequently occurred. The majority of herding passes and prey-capture attempts were subgroup behaviors that included a median of 2-3 dolphins. I found no evidence that doing herding passes in subgroups (or in larger subgroups) makes it less likely that a dolphin will attempt a prey capture. However, one benefit of performing prey-capture attempts in subgroups is that prey can be trapped between dolphins (similar to McMahon and Evans 1992; Gazda et al. 2005), which likely makes it easier to capture that prey. In the present study, trapping of prey between dolphins occurred, as evidenced by dolphins doing prey captures on opposite

sides of the prey ball (e.g., pinwheeling formation), and dolphins swimming directly towards each other to trap prey between them (i.e., converging formation). These coordinated prey-capture formations that we observed provide examples of ways in which dolphin coordination during prey-capture attempts may make it easier for them to capture fish, and familiarity between dolphins may increase the effectiveness of these coordinated behaviors (similar to Ramp et al. 2010).

Prey-capture attempts typically occurred on the side of the prey ball at both locations, and dolphins were most likely to have a ventral body orientation toward the prey ball. A dolphin typically tilted its white belly towards the prey ball briefly when it attempted to capture prey. A ventral body orientation may make it easier for a dolphin to see a fish during prey capture because the visual fields of a dolphin's right and left eye overlap in the region just under the front of their jaw (Norris et al. 1994). A dolphin can therefore best see a fish if the fish is in the region just under the front of the dolphin's jaw. Alternatively, a ventral body orientation may make it easier for a dolphin to echolocate on a fish during prey capture. When dolphins locate a fish via echolocation, their signals are directed forward from their melons (Au 2009; Au et al. 2010a), which are located dorsal to their mouths. If a dolphin determined the location of a fish then did a 180° spin, it would then be able to capture that fish. Finally, the white coloration of a dolphin's belly may facilitate prey capture by helping to hide the predator from prey (Würsig et al. 1990), but only if the dolphin is situated over the prey ball. Similarly, light coloration on the right side of fin whales seems to facilitate prey capture, since they

tilt the white-colored right sides of their lower jaw towards prey during feeding lunges (de Guevara 2008; Aguilar 2009).

However, in Argentina, a greater proportion of prey-capture attempts occurred through the edge or through balls and a smaller proportion occurred on the side of prey balls. Additionally, a similar proportion of prey-capture attempts were complementary in Argentina and NZ; however, in Argentina complementary attempts were most likely to be converging whereas in NZ they were most likely to be pinwheeling. Differences in prey-capture behaviors between study locations may be due to differences in what behaviors are most effective when feeding on large versus small prey balls. Since Argentina dusky dolphins more frequently encounter large prey balls, their prey-capture repertoire likely consists of tactics that they can use to effectively capture prey from a portion of a large prey ball. These tactics are more likely to involve swimming through prey balls, including doing coordinated converging tactics. Conversely, since NZ dusky dolphins more often encounter small prey balls, their prey-capture repertoire likely consists of tactics that can be used to effectively surround prey balls, and then capture fish from the sides.

How did dolphin group size relate to dolphin behaviors?

In NZ, as dolphin group size increased, I found evidence for coordinated feeding benefits and crowding-related costs (Acevedo-Gutiérrez 2009). As group size increased, herding passes occurred more closely together in time and passes were more likely to occur at the bottom of prey balls and less likely to occur on the top. Herding passes with a shorter timing between them may better contain the prey ball, and when a greater

proportion of herding passes occur on the bottom of the prey ball, the prey ball may move closer to the surface (Vaughn et al. 2008). Dolphins may tend to capture prey from the top or side of a prey ball because it may be easier since there is more sunlight, whereas dolphins may shift the location of those attempts to the bottom of the prey ball when they feed in larger groups due to increased crowding around the prey ball. Additionally, larger dolphin groups were more likely to attempt prey captures with a medium degree of coordination, and were less likely to attempt captures with no coordination. This may have simply been related to an increase in crowding around the ball during feeding as group size increased. However, a potential benefit of this increased number of prey-capture attempts by dolphins that occurred closely together in space and time is that the fish had fewer escape options, which may have made them easier to capture.

How did prey ball size relate to dolphin behaviors?

This study suggests that dusky dolphins show a tendency to feed on smaller prey balls. In Argentina, dolphins were more likely to attempt a prey capture when they were in the vicinity of a small prey balls than when they were in the vicinity of larger prey balls. In NZ, when dolphins fed on small prey balls, there was a trend ($P = 0.062$) for them to do more herding passes per dolphin per interval, which suggests that there was more feeding activity around small prey balls. There may be greater benefits of feeding on these prey balls. Smaller prey balls appear to be easier to contain (Vaughn et al. 2010b), and they may represent a space in which it is easier to capture fish because of a reduced confusion effect (Norris and Schilt 1988), increased fish exhaustion (Würsig

1986), or because dolphins can more readily trap fish between themselves (similar to Gazda et al. 2005). Killer whales off Norway showed a tendency to feeding on smaller schools of herring (*Clupea harengus*; Similä 1997; Nøttestad and Axelsen 1999), and predatory yellow amberjack fish (*Seriola lalandei*) have been observed splitting schools of jack mackerel (*Trachurus symmetricus*) and grunt (*Lythrulon flaviguttatum*) into smaller schools during foraging (Schmitt and Strand 1982). Cichlids (*Aequidens pulcher*) were more successful at attacking guppies (*Poecilia reticulata*) when they fed on smaller schools (Krause and Godin 1995), which suggests that these size-related tendencies are likely related to increased hunting success when feeding on small prey balls. One cost of foraging for smaller schools is that they are less conspicuous and thus more difficult to locate.

In NZ, prey ball size was related to location of prey-capture attempts. Dolphins were more likely to capture fish by swimming through prey balls when prey balls were larger, and there was a trend ($P = 0.069$) for dolphins to be less likely to capture fish from the sides of prey ball when they fed on smaller prey balls. Prey-capture attempts on the side of a prey ball are less disruptive to prey balls, which may make it less likely that a prey ball will become mobile. Additionally, a dolphin group is able to conduct more prey-capture attempts at the same time from a ball if they attempt to capture from the side, rather than by swimming through the ball. Despite these benefits, it may be harder for dolphins to capture fish from the side when they feed on large prey balls. Predatory fish, that often attack fish schools individually, typically swim through prey balls to capture fish (Schmitt and Strand 1982; Parrish 1993). Swimming through balls

may help predators to temporarily break up a fish school (and especially a large school), thus making it easier for them to focus on an individual fish by reducing the confusion effect (Norris and Schilt 1988).

How did ecology versus social learning relate to foraging behaviors?

Overall, ecology related to prey herding and capturing behaviors on a broad scale, while social learning differences between locations were evident on a finer scale. To examine how ecology related to bait-balling behaviors, I looked for within-site behavioral variations that were similar to between-site variations, and we found similarities with respect to herding pass location, prey-capture body orientation, and prey-capture location. Within NZ, dolphins in larger groups did a greater proportion of herding passes by the bottom of prey balls, and a greater proportion of attempts had a dorsal body orientation. Similarly, in Argentina, where dolphin groups were larger, dolphins did a greater proportion of herding passes by the bottom of prey balls, and a greater proportion of attempts had a dorsal body orientation, than in NZ. For prey-capture locations, when dolphins in NZ fed on larger prey balls, they did a greater proportion of prey-capture attempts by swimming through prey balls. Similarly, in Argentina, where prey balls were larger, dolphins did a greater proportion of attempts by swimming through prey balls than they did in NZ. To examine how social learning factors related to behavioral variations, I looked for within-site behavioral variations that were different from between-site variations. The only parameters that met these criteria were the occurrence of somersaulting in Argentina and type of coordinated prey-capture formation. Dolphins in Argentina typically used converging formations, whereas

dolphins in NZ typically used pinwheel formations. Broad prey herding and capturing behaviors likely are adaptive for containing and feeding on schooling fishes, and differences between locations in broad behaviors may reflect herding and capturing specializations that are a result of long-term learning specific to the ecological context of each location. Fine-scale differences in herding and capturing behaviors between locations may further represent specific adaptations to the ecological context of each location, or they may simply indicate alternative tactics.

CHAPTER III

DOLPHIN BAIT-BALLING BEHAVIORS IN RELATION TO PREY BALL ESCAPE BEHAVIOR*

Introduction

Escape tactics of prey co-evolve with foraging tactics of predators (Krebs and Davies 1993). Coordination between prey individuals can facilitate their escape or make it harder for predators to contain or capture them. Similarly, coordination between individual predators can make it easier for them to locate, contain, or capture prey. In marine environments, coordination by prey often occurs within schools (e.g., schools of fish, cephalopods, crustaceans). Schools can contain thousands of individuals that synchronize movements, which can facilitate effective anti-predation behaviors (Pitcher and Wyche 1983; Norris and Schilt 1988; Domenici and Batty 1994). Predators often feed on schooling prey by coordinating their own behaviors, although optimal sizes of predator groups likely depend on factors such as sizes of prey schools (Elgar 1989), prey distribution (Eggers 1976), and degree of coordination between predators (Burgess and Shaw 1979).

Schooling fishes reduce their chances of being eaten via schooling behaviors or escape (lateral or downward). Schooling behaviors allow individuals to react more effectively to an attack due to synchronized school movements (Domenici and Batty

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1997; Gerlotto et al. 2006), including movements of the fish school around an attacking predator (e.g., vacuole formations, Pitcher and Wyche 1983). Schooling behaviors can also make it harder for predators to capture prey due to the confusion effect, which makes it hard for to the predator to focus on an individual fish to capture it (Norris and Schilt 1988). The confusion effect likely increases with school size (Litvak 1993), which may be why it is more difficult for predators to capture fish from larger schools (Neill and Cullen 1974; Krause and Godin 1995).

Fish may be better able to escape from predators when they form larger schools because it is harder for predators to contain large schools against barriers (e.g., the surface, shore, or other predators; Vaughn et al. 2010b). Larger schools present more surface area for predators to surround when they try to contain prey against a barrier, and thus prey would be better able to escape towards the non-surrounded side of the prey ball. Lateral escape may be more effective for small prey balls, since they may be more difficult for predators to re-locate (Krause and Godin 1995). However, downward escape may be more effective for larger prey balls, since air-breathing predators such as dolphins, pinnipeds, or seabirds would have a more difficult time accessing a deeper prey ball (Heithaus and Dill 2009).

Marine predators such as dolphins counter these anti-predation tactics in part by using coordinated prey herding or capturing behaviors (Wells et al. 1999; Connor 2000; Heithaus and Dill 2009). At times, dolphins coordinate behaviors to herd prey against a barrier such as the surface of the water, which prevents prey from escaping while also facilitating prey capture (Hoese 1971). Coordinated herding may also function in

moving prey in a particular direction, such as closer to the surface (Similä and Ugarte 1993; Fertl and Würsig 1995). It is beneficial to dolphins for prey to be closer to the surface not just because it can serve as a barrier, but also because it reduces travel time from the surface to the prey ball. Prey balls that are closer to the surface are also more visible since there is more sunlight closer to the surface, which may make it easier to capture prey. Dolphins also coordinate behaviors to capture prey by sandwiching prey between 2 or more dolphins (Gazda et al. 2005), which reduces escape options for fish. Finally, predatory fish at times split prey balls so that they are smaller and thus easier to contain or to capture prey from (Schmitt and Strand 1982); however, this behavior has not been described for dolphins.

Dusky dolphins are a southern hemisphere delphinid that is distributed over the Continental Shelf in temperate latitudes, mainly off South America, NZ, and western Africa (Würsig et al. 2007). They feed via two general habitat-dependent tactics: at nighttime on deep scattering layer lanternfishes and squids (e.g., off Kaikoura, NZ; Dahood and Benoit-Bird 2010), and during daytime in shallow bays on schooling fishes (mainly from the Order Clupeiformes; Vaughn et al. 2010a). While they coordinate behaviors during both types of foraging tactics, coordinated foraging behaviors have been studied with most detail in Admiralty Bay and adjacent Current Basin, NZ (McFadden 2003; Benoit-Bird et al. 2004; Markowitz et al. 2004; Pearson 2009; Vaughn et al. 2007, 2008, 2010a). Here, they, at times, coordinate behaviors to herd schooling fishes towards barriers. They most frequently herd prey towards the surface, but they also have been observed herding prey towards the shore or against a boat (Duffy and

Brown 1994; McFadden 2003). During the present study, when focal dusky dolphin groups fed on schooling fishes, mean group size was 8 ± 5 dolphins, and mean duration of feeding was 5 ± 6 min (Vaughn et al. 2007). Observed prey ball sizes were a mean of 8 ± 6 m^2 (Vaughn et al. 2007).

Despite the frequency with which dusky dolphins coordinate behaviors to herd and capture prey in Admiralty Bay and Current Basin, the behaviors that they use to contain prey balls have seldom been characterized systematically (but see Chapter II), and we know little about the contexts in which they try to contain prey (e.g., prey occurring at different depths). Prey ball behaviors during dolphin feeding bouts have been generally described (Vaughn et al. 2008, 2010a), but not in relation to dolphin herding and prey-capturing behaviors, to our knowledge. This information increases our understanding of proximate costs and benefits of foraging behaviors, and how they relate to ecological context.

My objectives here were to 1) describe prey ball escape behaviors and 2) investigate how prey ball behaviors related to dolphin prey herding and capturing behaviors. I described vertical prey escape behaviors directly, and I quantified dolphin foraging behaviors as indicators of horizontal and vertical prey escape behaviors. I quantified dolphin prey herding and capturing behaviors above-water and underwater.

Methods

Study site and data collection

This study occurred in Admiralty Bay (40°57'S, 173°55'E), and Current Basin (40°57'S, 173°48'E), NZ. Above-water data were recorded from 5 August to 4

November, 2005 and from 22 May to 28 August, 2006. The methods that were used to locate and follow dolphin groups were the same as those used in Chapter II. During focal follows of dolphin groups, I recorded above-water data at 2-min intervals that included location, group size, predominant behavior, and number of leaps per 2-min interval (in 2005 only).

Location was recorded using a hand-held Garmin Model 76 GPS unit. Group size was determined by including all dolphins within 10 m of another dolphin (Smolker et al. 1992). Predominant behavior was defined as the behavior exhibited by the majority of the group for the majority of the 2-min interval (Table 1). I categorized feeding behavior during each 2-min interval as mobile (moving horizontally) or stationary (not moving horizontally). Although dolphins spend a large proportion of their time underwater, above-water behaviors are a useful proxy for underwater behaviors (Acevedo-Gutiérrez and Parker 2000). I determined the predominant behavior of the group during each interval by observing the behavior of each individual as they surfaced throughout the interval. Although there were differences between behaviors in their visibility, I categorized group behavior according to what behavior the majority of the group exhibited for the majority of the interval. Leaps were categorized as one of 3 types (Table 2). Above-water dolphin data were recorded by one observer, while I followed the dolphins at a distance of 25-50 m.

Table 1. Definitions of dolphin predominant behaviors.

Behavior	
Feed	High-level activity that changed direction frequently and that included leaping or burst swims.
Rest	Meandering movement or directed movement < 3 knots.
Social	Acrobatic or touching behavior.
Travel	Horizontal movement that was mainly in one direction and ≥ 3 knots

Table 2. Definitions of dolphin leap types.

Behavior	
Clean	Entire body of dolphin leaves the water, then re-enters head-first, making little noise.
Coordinated	2 or more dolphins do clean leaps close to each other and at the same time.
Noisy	Entire body of dolphin leaves the water, then re-enters by landing on its' side, making a noisy splash.

During stationary feeding bouts, 1-2 observers recorded underwater data using the same methods as were used in Chapter II. I recorded the depth of the middle of the prey ball from the surface at 2-min intervals using a dolphin length as a reference (1.73

m, *sensu* Cipriano 1992). I recorded underwater video footage with a Sony DCR-HC1000 videocamera in an Amphibico housing. Underwater data and video footage were temporally synchronized with above-water focal follow data.

Underwater behavioral quantification

I analyzed prey herding and capturing behaviors of dolphins across 1-min underwater feeding intervals by doing focal follows on all dolphins that swam within 2 m of the prey ball. Chapter II definitions were used to quantify herding pass and prey-capture parameters, including location of each herding pass, location of each prey-capture attempt, body orientation for each complete herding pass, and body orientation for each prey-capture attempt that occurred on the side of the prey ball. For each prey ball, I quantified the two-dimensional area with Image J (http://rsb.info.nih.gov/ij/), using the mean length of an adult dusky dolphin as a size reference (1.73 m, *sensu* Cipriano 1992). I also characterized the occurrence of funneling, which I defined as a prey ball shape where the height of the prey ball was at least twice its' width. Prey ball changes in depth and general shape were recorded pre-funneling and post-funneling.

Behavioral analyses

A feeding bout was defined as a continuous and discrete period of feeding. Locations of feeding bouts were mapped with ArcView GIS version 3.3 (Environmental Systems Research Institute, Inc., Redlands, California). Distances traveled during feeding bouts were measured using Garmin MapSource version 6.12.4. Dolphin group sizes were calculated for each 2-min feeding interval, as the median number of dolphins

that were present at the start and at end of each interval. I categorized prey balls as small (< 6 m^2) or large (≥ 6 m^2) to be consistent with previous studies (Vaughn et al. 2010b).

I analyzed occurrence and number of different leap types per 2 min feeding interval, and number of leaps per median dolphin group size per 2 min feeding interval, to provide information on depth of prey (clean leaps) and degree of coordination or communication between individuals (coordinated and noisy leaps). Dolphins use clean leaps to quickly take a breath before returning to depth (Würsig and Würsig 1980; Acevedo-Gutiérrez and Parker 2000; Würsig and Whitehead 2009). In Admiralty Bay, dusky dolphins most often exhibit clean leaps during feeding (Pearson 2009), which suggests that they use this leap type to return to depth to contain or capture prey. Thus, analyzing clean leaps during feeding provides a useful proxy for depth of prey. Although coordinated and noisy leaps are used in diverse behavioral contexts, they most often suggest coordination and communication between individuals, respectively (Würsig and Whitehead 2009), which makes them useful proxies.

For each feeding bout, I categorized vertical movement of a prey ball as "ascending" ($N = 10$), "constant-depth" ($N = 18$), or "descending" ($N = 9$), based on overall change in depth of the prey ball between the start and end of the feeding bout (Vaughn et al. 2010b). "Ascending" prey balls ascended ≥ 2 m and this was their main direction of movement; "constant depth" prey balls ascended or descended ≤ 1 m consecutively; and "descending" prey balls descended ≥ 2 m.

To investigate how prey ball behaviors related to underwater dolphin behaviors, I compared dolphin behaviors during 1-min intervals when prey balls were ascending to

1-min intervals when they remained at a constant depth. Since all prey balls that ascended were small, I only compared dolphin behavioral data from these feeding bouts to constant-depth prey balls that were also small. I summarized herding and prey-capture parameters by calculating parameters and percentages of individual behaviors, and by quantifying numbers of behaviors per interval.

I did not include data on numbers of multi-species feeding associates in analyses due to small underwater sample sizes. I did not include data on prey species in analyses because I was only able to identify prey species during 2 feeding bouts (when prey was pilchard, *Sardinops* spp., Vaughn et al. 2007).

Statistical analyses

I used SPSS 13.0 for Mac OS X software (SPSS Inc., Chicago, IL) for statistical analyses. I used non-parametric statistics to analyze data due to small sample sizes. To examine relationships between variables, I used Chi-square (CS) and Mann-Whitney U (MW) tests, depending on if I was analyzing categorical or numerical variables. I used Wilcoxon Signed Ranks tests (WS) to analyze behavioral changes that occurred in consecutive feeding intervals during a single feeding bout. Feeding bouts were considered to be independent, because they occurred at different times on different prey balls. We used a 2-tailed alpha level of 0.05. We present descriptive statistics as medians ± interquartile ranges (IQR).

Results

During this study, I collected data on 99 days. I followed dolphin groups for a total of 201 h during 171 focal follows. Overall, dolphins were feeding during 16.5%,

traveling during 13.5%, resting during 44.5%, socializing during 11%, and doing other or unknown behaviors during 14.5% of 2-min intervals (N = 5620 intervals). I recorded above-water data from 335 feeding bouts, and underwater data for 52 of those feeding bouts.

Table 3. Number of feeding bouts and thus prey balls that were horizontally mobile versus stationary at start of feeding and during later 2-min feeding intervals. Numbers in parentheses include only those feeding bouts for which we observed the start of dolphin feeding. FB = feeding bout.

1st feeding interval, N = 335 (209) FB	**Later in feeding**
236 (209) mobile	**19** (15) became stationary **217** (194) did not become stationary
81 (66) stationary **18** (15) unknown	

Horizontal prey movements

Dolphin horizontal movements during feeding indicated horizontal movements by prey. The majority of dolphin feeding bouts were mobile during the first 2-min interval (Table 3), and only 8% of feeding bouts that were mobile during the first 2-min interval became stationary in subsequent 2-min intervals (Table 3, Figure 9). Feeding bouts that were mobile before they were stationary were mobile for one 2-min interval (range = 1-7, N = 15 feeding bouts). Distance that the boat traveled during mobile

dolphin feeding intervals was 82 m per interval (IQR = 44-153, N = 15 feeding bouts), while distance that the boat traveled during subsequent stationary dolphin feeding intervals was 42 m per interval (IQR = 36-65, N = 15 feeding bouts).

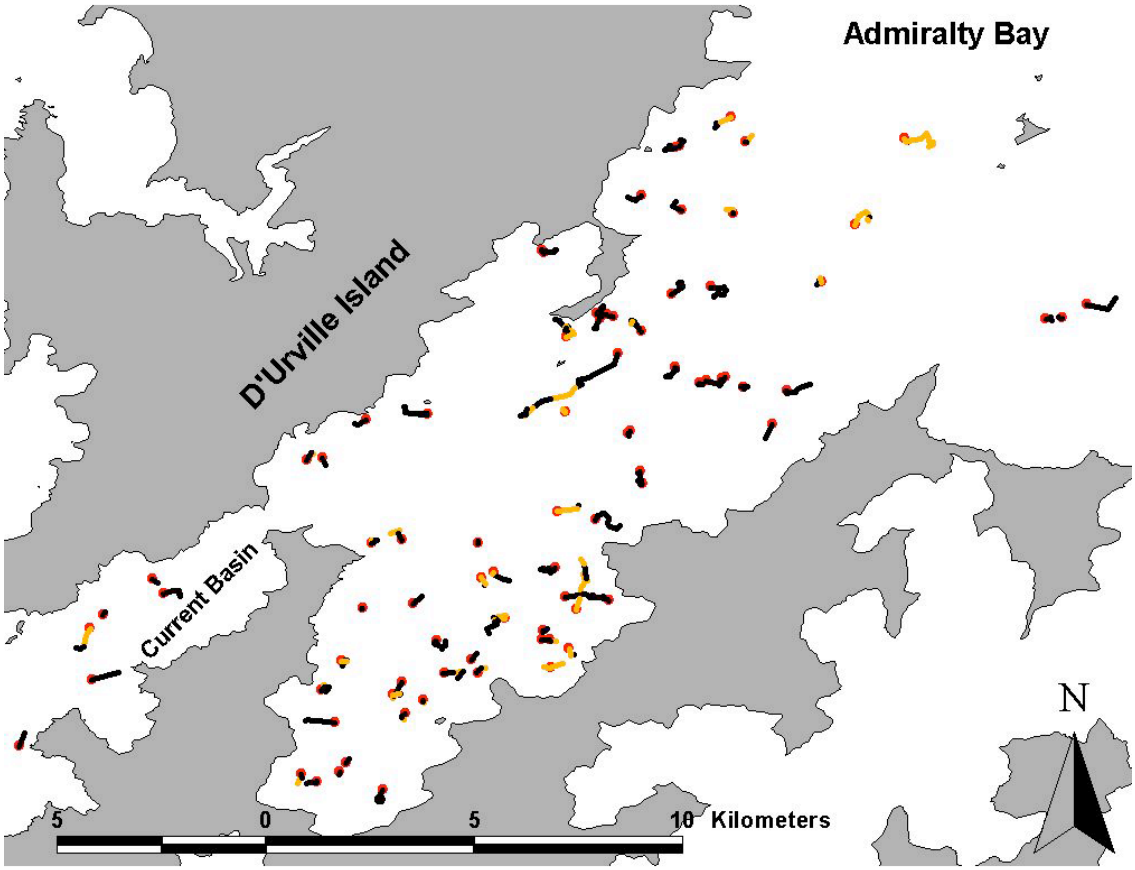

Figure 9. Paths traveled by the boat during feeding bouts that were stationary at some time (N = 84 feeding bouts). Orange lines indicate 2-min intervals during which feeding behaviors were mobile, while black lines indicate 2-min intervals during which feeding behaviors were stationary. Red dots indicate starting locations for feeding bouts. The above map shows only feeding bouts for which we observed the start of feeding.

There were no differences in dolphin horizontal movements between feeding bouts in which only mobile behaviors occurred, and feeding bouts in which mobile behaviors occurred during early 2-min intervals and stationary behaviors were present during later 2-min intervals. Considering only those dolphin feeding bouts for which we observed the start of feeding, there was no difference in distance that the boat traveled per 2-min mobile feeding interval between feeding bouts that were later stationary (N = 15 feeding bouts), and feeding bouts that did not become stationary (N = 155 feeding bouts) (MW test: Z = -1.055, P = 0.291). There was also no difference in the number of intervals that feeding bouts were mobile between feeding bouts that were later stationary (N = 15 feeding bouts), and feeding bouts that did not become stationary (N = 194 feeding bouts) (MW test: Z = -0.582, P = 0.561).

Prey depth and vertical prey movements

When dolphin feeding started, prey was at times already at the surface (during the first 2-min feeding interval of at least 11 of 335 feeding bouts). But more often, prey appeared to be deeper, as indicated by dolphins exhibiting long surface intervals, and doing clean leaps. Long surface intervals occurred during the first 2-min feeding interval for at least 50 of 335 feeding bouts, and at least one clean leap occurred during the first 2-min feeding interval for 102 of 162 feeding bouts for which leaps were recorded.

Prey depth did not differ between mobile and subsequent stationary feeding intervals, based on clean leap parameters. For mobile feeding bouts that later became stationary, and taking into consideration only those feeding bouts for which we observed

the start of feeding, there was no difference between mobile and subsequent stationary feeding intervals in the occurrence of clean leaps (WS test: Z = -1.414, $P = 0.157$). At least one clean leap occurred during 12 of 14 (86%) mobile feeding intervals, and during 14 of 14 (100%) subsequent stationary intervals. There was also no difference between mobile intervals and subsequent stationary intervals in number of clean leaps per dolphin per interval (WS test: Z = -0.157, $P = 0.875$, $N = 12$ feeding bouts).

Prey depth also did not differ between mobile feeding bouts that became stationary in later 2-min intervals and feeding bouts that did not become stationary, based on clean leap parameters. There was no difference in occurrence of clean leaps between mobile feeding bouts that became stationary and those that did not (CS test: $X^2 = 0.633$, $P = 0.426$). At least one clean leap occurred during the mobile portion of feeding for 12 of 14 (86%) mobile feeding bouts that became stationary (considering only those feeding bouts for which we observed the start of feeding), and 43 of 57 (75%) mobile feeding bouts that did not become stationary. There was also no difference in number of clean leaps per dolphin per mobile interval during feeding bouts that became stationary ($N = 12$ feeding bouts) than during feeding bouts that did not ($N = 53$ feeding bouts; MW test: Z = -1.860; $P = 0.063$).

Figure 10. Photos showing the most extreme funnel shape (i.e., greatest height to width ratio) that I observed during each of the 5 feeding bouts for which funneling was observed.

Descending appeared to be a vertical escape behavior exhibited by prey balls. In total, 9 of 37 prey balls that I observed for at least 2 min descended ≥ 2 m. The only obvious prey ball escape behavior that I observed prior to descending was the formation of a funnel shape (Figure 10), and 5 prey balls formed funnel shapes on 29 occasions.

Funneling was most commonly observed for large prey balls that exhibited overall descending behavior (Table 4), but prey balls overall were more likely to descend without forming a funnel shape (6 of 9 descending prey balls did not form funnel shapes; these 6 non-funneling prey balls descended 8 times). A total of 6 of 29 funnels descended post-funneling. Duration of observed funneling was 11 s (IQR = 5-18, range = 3-40, N = 29 occurrences; Figure 11). There was no obvious change in the velocity or acceleration of fish within the prey ball during funneling; however, it was not possible to quantify fish speeds due to insufficient video clarity.

Table 4. Size and behavioral parameters for prey balls that formed funneling shapes. Prey ball numbers in this table correspond to numbers in Figure 2.

Prey ball #	Size	# times funneled	Overall movement of prey ball
1	Large	12	Descending (≥ 16 m in 2-min)
2	Large	5	Descending (≥ 8 m in 2-min)
3	Large	10	Descending (3 m in 2-min)
4	Small	1	Constant depth
5	Small	1	Ascending

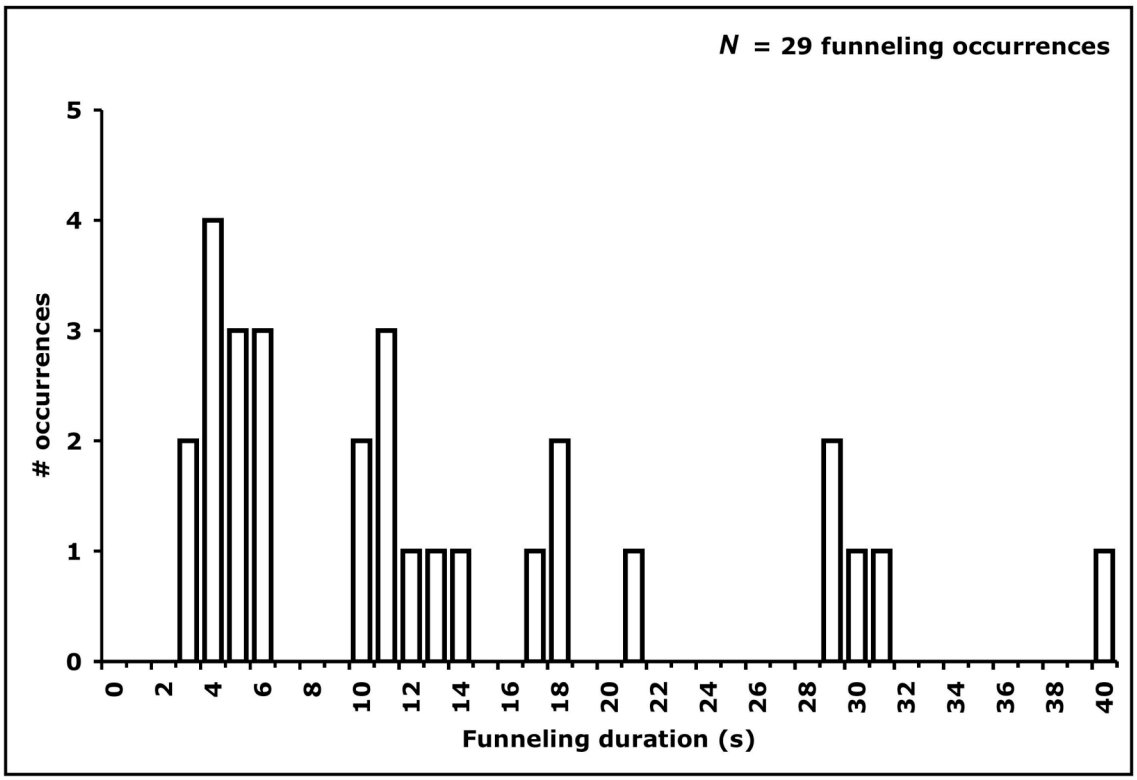

Figure 11. Distribution of durations of funneling (occasions when prey balls had a height that was at least twice their width). Data are during 5 dolphin feeding bouts.

Behaviors of prey balls before and after funneling were related to overall prey ball behaviors. For prey balls 1 and 2, prey appeared to form a funnel shape as an escape behavior, since this formation often preceded rapid descending movements. Of the 37 prey balls that we observed for at least 2 min underwater, prey balls 1 and 2 were the largest (18 m^2 and 16 m^2, respectively), and they exhibited the most rapid descending behaviors. No other obvious factors appeared to contribute to the rapid descending behaviors of these 2 prey balls (e.g., presence of other predators). For prey ball 1, pre-funneling, the prey ball was either at or within 5 m of the surface (N = 8 and 4 funneling occasions, respectively). Post-funneling, the prey ball either descended out of sight or

returned to a roughly circular shape at or within 5 m of the surface (N = 3, 7, and 2 occasions, respectively). For prey ball 2, pre-funneling, the prey ball was at the surface on all occasions. Post-funneling, the prey ball either descended out of sight or returned to a roughly circular shape at the surface (N = 2 and 3 occasions, respectively). Prey ball 3 also exhibited overall descending movement during dolphin feeding and was large (14 m^2). However, when this prey ball descended, it did so much less rapidly (Table 5). When prey ball 3 formed a funnel shape, it was a brief change in shape that did not precede any changes in behavior of the prey ball. Pre-funneling and post-funneling, this prey ball was on all occasions 2-4 m below the surface. Prey balls 4 and 5 only formed a funnel shape on one occasion each. For both prey balls, funneling occurred when the prey balls were ascending but within 2 m of the surface, and funneling seemed to be due to the prey balls stretching towards the surface.

Prey ball behaviors in relation to dolphin prey herding and capturing behaviors

After locating prey, dolphins often exhibited leaping, diving, or burst swimming, such that they appeared to be rapidly swimming after or trying to contain prey, and capture attempts were likely also occurring at this time. Coordination of behaviors used to rapidly swim after, contain, and capture prey at times occurred. For example, on 2 occasions, dolphins were traveling slowly for a long time, then they spread out and began burst swimming, which suggests intra-group coordination of prey containment or capturing behaviors. On at least 2 other occasions, 2 dolphin groups burst swam towards the same location, suggesting inter-group coordination, also likely relative to containing or capturing prey.

I analyzed number of coordinated and noisy leaps per feeding interval as indicators of degree of coordination or communication between individuals, respectively. Considering only those feeding bouts for which we observed the start of feeding, there was no difference between feeding bouts that became stationary (N = 13 feeding bouts) and those that did not (N = 53 feeding bouts) in number of noisy (MW test: Z = -0.413, P = 0.680) or coordinated (MW: Z = -0.768, P = 0.442) leaps per dolphin per mobile interval. At least one coordinated leap occurred during 4 of 13 (31%) feeding bouts that became stationary and 18 of 53 (34%) feeding bouts that did not; at least one noisy leap occurred during 2 of 13 (15%) feeding bouts that became stationary and 9 of 53 (17%) feeding bouts that did not. For feeding bouts that became stationary, there was no difference between mobile and subsequent stationary intervals in number of coordinated (Z = -1.689, P = 0.091) or noisy (Z = -1.342, P = 0.180) leaps per dolphin (WS tests; N = 13 feeding bouts). At least one coordinated leap occurred during 4 of 13 (31%) mobile portions of these feeding bouts, and 9 of 13 (69%) stationary portions. At least one noisy leap occurred during 2 of 13 (15%) mobile portions of these feeding bouts; noisy leaps did not occur during any stationary portions.

I analyzed dolphin herding data for 5 prey balls that ascended during 6 1-min intervals, and 5 prey balls that remained at constant-depth during 24 1-min intervals. Herding behavior sample sizes for descending prey balls were too small for me to include them in this comparison. For feeding bouts where prey balls were ascending, a smaller proportion of herding passes occurred on the bottom of prey balls than during feeding bouts where the prey ball remained at constant depth (Z = -2.095, P = 0.036),

but there was no difference between ascending and constant-depth prey balls in proportion of passes that occurred on the side ($Z = -0.841$, $P = 0.401$) or top ($Z = -1.051$, $P = 0.293$) of the prey ball (MW tests). For ascending prey balls, proportion of herding passes that occurred on the bottom of prey balls was 0.3 (IQR = 0.1-0.3, range = 0-0.3); for constant-depth prey balls, proportion of herding passes that occurred on the bottom was 0.4 (IQR = 0.3-0.4, range = 0.3-0.5). There was no difference between ascending and constant-depth prey balls in number of herding passes per interval ($Z = -0.104$, $P = 0.917$), number of herding passes per dolphin per interval ($Z = -1.470$, $P = 0.142$), or proportion of herding passes that included a prey-capture attempt ($Z = -1.676$, $P = 0.094$) (MW tests).

I quantified dolphin prey-capture data for 6 prey balls that ascended during 9 1-min intervals, and 5 prey balls that remained at constant-depth during 27 1-min intervals. Prey-capture behavior sample sizes for descending prey balls were too small for me to include them in this comparison. For feeding bouts where prey balls were ascending, there was a larger proportion of prey-capture attempts that occurred on the side of the prey ball ($Z = -2.395$, $P = 0.017$), and a smaller proportion of attempts where the dolphin swam through the edge of the prey ball ($Z = -2.091$, $P = 0.037$); there was no difference in proportion of attempts where the dolphin swam through the prey ball ($Z = -1.692$, $P = 0.091$) (MW tests; Figure 12a). For ascending prey balls, when dolphins did prey-capture attempts on the side of the prey ball, they were less likely to have a dorsal body orientation towards the prey ball ($Z = -2.090$, $P = 0.037$); there was no difference in proportion of attempts with a side ($Z = -1.647$, $P = 0.100$) or ventral ($Z = -1.742$, $P =$

0.081) body orientation (MW tests; Figure 12b). There was no difference between ascending and constant-depth prey balls in number of prey-capture attempts per interval ($Z = 0.000$, $P = 1.000$), or number of attempts per dolphin per interval ($Z = -1.358$, $P = 0.175$) (MW tests).

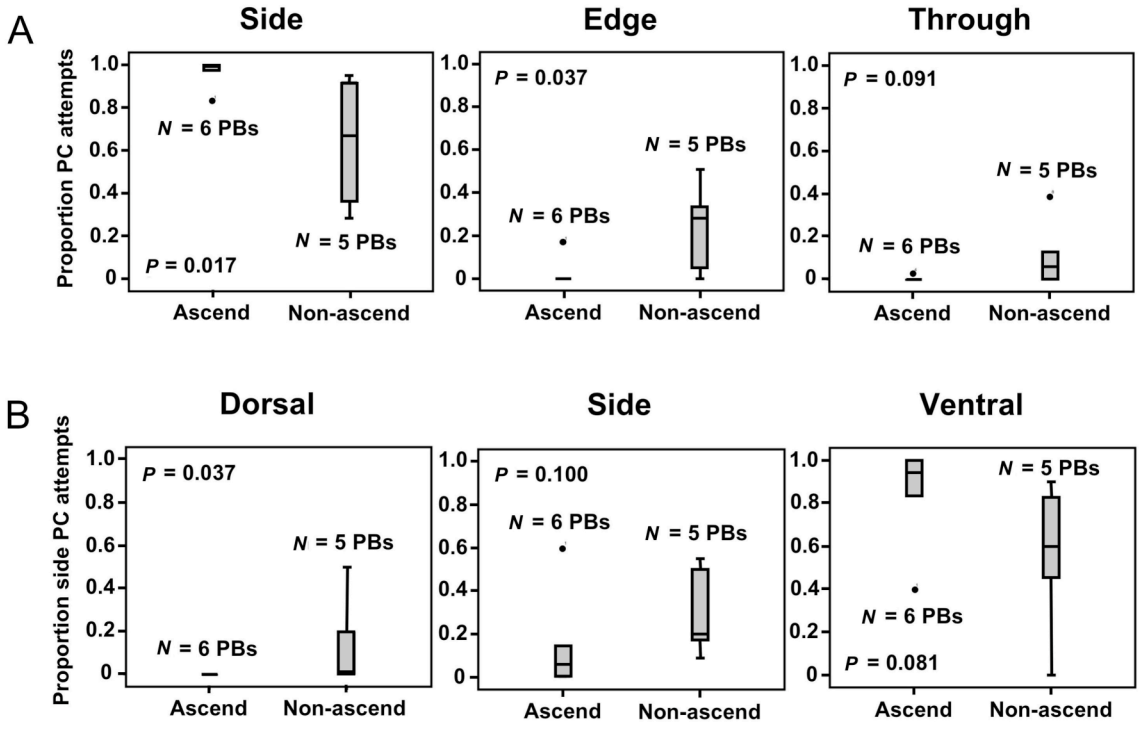

Figure 12. Proportion of dolphin prey-capture attempts that occurred on the side, through the edge, or through the prey ball (A), and on the side of the prey ball for which dolphin body orientation towards the prey ball was dorsal, side, or ventral (B), for ascending compared to constant-depth prey balls. Lines show medians, boxes show IQRs, error bars show ranges, and dots show outliers. PB = prey ball. *P* values are from Mann-Whitney U tests.

Discussion

Prey balls exhibited horizontal and vertical movements, which likely represented escape behaviors. I described the occurrence of funneling, a distinct behavior that was most often observed for larger prey balls just before they descended. This study also provided insights into how prey ball behaviors related to dolphin prey containment and capture behaviors.

Prey ball escape behaviors and apparent foraging costs and benefits for dolphins

Prey balls frequently exhibited horizontal movements, which likely resulted in increased feeding costs for dolphins, since a dolphin would expend more energy feeding on a horizontally moving prey ball than it would feeding on a stationary prey ball. Most prey balls were horizontally mobile at the start of dolphin feeding, and most of these prey balls remained mobile throughout feeding. Dolphins were thus either unable to, or not interested in, containing these prey balls. It may not have been worthwhile for dolphins to contain prey for most feeding bouts because feeding bouts were short in duration (mean = 5 min, Vaughn et al. 2007).

When prey balls that were mobile became stationary, they became stationary rapidly and within short distances, which suggests either that dolphins readily contained them or that prey balls became stationary on their own (e.g., due to dolphin prey-capture behaviors, or due to prey seeking refuge in a particular location such as at the surface). When dolphins fed on mobile prey balls, there was no difference between prey balls that became stationary and those that did not in how long or how far dolphins chased prey when it was mobile. This suggests that prey parameters rather than dolphin herding

efforts determined whether or not prey balls became stationary. For example, prey ball size or numbers of associated predators may affect how likely a prey ball is to become stationary. Larger prey balls may be less likely to become stationary during dolphin feeding bouts due to school size-related emergent properties of fish schools (Viscido et al. 2005; Vaughn et al. 2010b). Prey balls also may be less likely to become stationary when there are fewer diving seabirds such as gannets or shearwaters (*Puffinus* spp.; Vaughn et al. 2010b), due to reduced disruption of prey balls.

Prey balls typically appeared to be at depth at the start of dolphin feeding bouts, and I found no strong evidence to indicate that prey depth differed between prey balls that became stationary and those that did not, or between mobile and stationary portions of feeding bouts. There was an insignificant trend ($P = 0.063$) for there to be more clean leaps per dolphin per mobile interval for prey balls that became stationary than for those that did not. This suggests either that prey balls that later became stationary were initially deeper than those that did not, or that dolphins expended more energy vertically diving to prey for feeding bouts that later became stationary than for those that did not. The latter hypothesis is more logical. If this latter hypothesis is correct, then dolphins may have benefited most from feeding on or containing prey balls that later became stationary, either because those prey balls had characteristics that made it easier to contain them or because they had characteristics that facilitated prey capture (e.g., characteristics relative to prey ball size, Schmitt and Strand 1982; Nøttestad & Axelsen 1999; depth, Similä 1997; species, Vaughn et al. 2010a; or multi-species associates, Heithaus 2001; Acevedo-Gutiérrez 2002; Vaughn et al. 2008).

During this study, the majority of prey balls that were observed underwater remained at constant depth during dolphin feeding (Vaughn et al. 2010b), although we also frequently observed prey balls to descend or ascend. Anti-predation behaviors of constant-depth prey balls appeared to focus on schooling close to the surface, which may be sufficient when the amount of feeding activity is low (Wirsing et al. 2010). Anti-predation behaviors at the level of individual fish were not examined in this study but likely occurred frequently as well (e.g., vacuole formations, Pitcher and Wyche 1983; schooling behaviors, Domenici and Batty 1997; Gerlotto et al. 2006).

Prey balls also exhibited downward vertical movements, which would have increased feeding costs for dolphins since they would then need to dive down to the prey ball. Descending escape behaviors of ≥ 2 m occurred for 9 of 37 prey balls that were horizontally stationary (Vaughn et al. 2010b). In this study, I described funneling prey ball shapes that at times preceded descending movements. Funneling was most often observed for very large (18 m^2, 16 m^2, and 14 m^2) prey balls that exhibited descending movements, and it was typically a brief behavior (median = 11 s). Besides funneling shapes that occurred before prey balls descended, funneling also occurred when 2 smaller prey balls were ascending, just before they reached the surface. Thus, funneling appears to be a transition shape that occurs in an anti-predation context, either due to prey attempting to rapidly descend, or due to prey attempting to rapidly reach the surface. When prey balls are unable to escape by descending, ascending to the surface may provide a barrier that could reduce the surface area from which prey experience predation attacks. Similar funneling prey ball shapes have been observed for other

schooling fishes (Pitcher and Parrish 1993), as well as in inanimate aggregations (Parrish et al. 2002), and schools of herring at times form a funneling shape before descending to escape predation by killer whales (Nøttestad and Axelsen 1999). Deeper waters would facilitate schooling fishes escaping by descending, and habitat choice decisions to occupy deeper waters may be a tactic that some schooling fish use to reduce predation risk (Heithaus et al. 2009).

Prey ball behaviors in relation to dolphin prey herding and capturing behaviors

After locating prey, dolphins at times coordinated behaviors, likely to try to contain or capture prey, and I described two examples of coordination of behaviors within and between groups. I found no difference in degree of coordination between feeding bouts that became stationary and those that did not, as indicated by number of coordinated leaps per dolphin. However, there was an insignificant trend ($P = 0.091$) for dolphins to do fewer coordinated leaps during mobile portions of feeding bouts than during subsequent stationary portions. When prey balls are mobile, coordination likely occurs at greater distances than when prey is stationary. When prey is stationary, coordinated leaps may indicate close-range coordination, which has also been for underwater behaviors (e.g., Similä and Ugarte 1993; Fertl and Würsig 1995). I found no relationships between horizontal mobility of prey and number of noisy leaps. However, few noisy leaps occurred, so longer-range communication may instead occur via less costly acoustic signals (Dudzinski et al. 2009).

When prey balls descended during dolphin feeding, funneling preceded vertical escape for some large prey balls. One might expect dolphin behaviors to change when

prey balls form a funnel shape, to prevent the prey ball from escaping. I at times observed dolphins swim under prey balls when they started to form a funnel shape, and this behavior at times appeared to have the effect of causing the prey ball to resume a circular shape at the surface. However, I was unable to quantitatively examine this relationship because prey balls were only visible for short durations when they were in funnel shapes.

Dolphin herding behaviors were related to ascending movements of prey balls. First, when prey balls ascended, a smaller proportion of herding passes occurred on the bottom of prey balls, but there was no difference in the total number of herding passes that occurred on the bottom of prey balls (MW test: $Z = -0.498$, $P = 0.730$). When larger groups fed on ascending prey balls, each dolphin therefore did fewer herding passes on the bottom of prey balls than when larger groups fed on constant-depth prey balls, possibly because less herding effort per dolphin was needed. This reduction in herding effort per dolphin as group sizes increase may have reduced the herding cost per dolphin in larger groups. Second, when prey balls ascended, there was an insignificant trend ($P = 0.094$) for a smaller proportion of herding passes to include a prey-capture attempt. This suggests that prey balls may be more likely to ascend when dolphins swim by prey balls without attempting a prey capture. Similar behaviors have been hypothesized to have herding functions for dusky dolphins off Argentina (Würsig 1986); other dolphins also herd prey including killer whales off Norway (Similä and Ugarte 1993), and Atlantic spotted dolphins (Martin 1986; Fertl and Würsig 1995).

Dolphin prey-capture behaviors were also related to ascending movements of prey balls. First, when prey balls ascended, a larger proportion of dolphin prey-capture attempts occurred on the sides of prey balls and a smaller proportion occurred through the edge of prey balls; there was also an insignificant trend ($P = 0.091$) for a smaller proportion to occur through prey balls. Second, when prey balls ascended and dolphins did prey-capture attempts on the sides of prey balls, there was an insignificant trend for them to more often face their ventral sides towards the prey ball ($P = 0.081$), and to less often face their sides towards the prey ball ($P = 0.100$); they also less often faced their dorsal sides towards prey balls. These patterns suggest that location of prey-capture attempt and dolphin body orientation influence ascending vertical movement of prey balls. Prey-capture attempts that occur on the side of the prey ball are likely less disruptive to the prey ball (Vaughn et al. 2010a). Prey-capture attempts where the dolphin orients its ventral side towards the prey ball may be most effective in concentrating or moving the prey ball, possibly by frightening or startling fish (Würsig et al. 1990). This effect is probably more pronounced when a dolphin swims under a prey ball because its white belly would be most visible, whereas a dolphin swimming over the prey ball with a ventral orientation would be least visible.

Conclusions

Horizontal and vertical movements of prey balls likely represented prey ball escape behaviors, and would have increased costs of feeding for dolphins. Most feeding bouts were horizontally mobile, and only a small proportion of mobile feeding bouts became stationary in later intervals. The small percentage of mobile feeding bouts that

became stationary suggests that prey ball parameters such as size or species of prey balls, or multi-species associates, affected whether or not prey balls became stationary more than did dolphin behaviors. For feeding bouts that did become stationary, I observed descending behaviors, and prey ball funneling formations occurred at times before large prey balls descended. Dolphins at times were observed to swim under prey balls when they formed funneling shapes. This may have been a tactic that prevented prey balls from subsequently descending, but I was unable to quantify occurrences of this behavior. Dolphin behaviors that were related to ascending movements of prey balls were herding passes that did not include a prey-capture attempt, and prey-capture attempts on the sides of prey balls with a ventral body orientation. Here, I analyzed dolphin behavioral data at the group rather than at the individual level, and differences in individual behaviors within a group would have differentially affected individual costs.

CHAPTER IV

CHARACTERIZING DUSKY DOLPHIN SIGNALS FROM ARGENTINA AND NEW ZEALAND

Introduction

Characterizing a species' acoustic signals allows us to subsequently investigate similarities and differences between species, populations, or behaviors, which in turn provides information on diverse types of questions. Between-species comparisons can provide information on evolutionary relationships (Greene 1994; Harvey and Pagel 2000). Population level comparisons increase our understanding of how ecology and culture influence a species' repertoire (Janik and Slater 2000). Behavioral comparisons increase our understanding of proximate functions of signals (e.g., Jones and Sayigh 2002; Bazúa-Durán and Au 2004); for example, different signal categories can at times be used for echolocation (Madsen et al. 2005), communication (Janik 2009), and manipulating prey during foraging (Simon et al. 2006).

Delphinid signals are typically categorized as whistles (i.e., tonal), click trains (i.e., clicks spaced farther apart), or burst pulses (i.e., more closely spaced clicks) (Dudzinski et al. 2009). Each of these categories has also been subcategorized via diverse qualitative and quantitative methods. The most appropriate method to use depends on the research question. Still, when characterizing a species' repertoire, quantitative methods are preferable since they facilitate between and within species comparisons. Additionally, we know little about how dolphins perceive signals; thus, it

is often unclear if our (human) subjective characterization methods are meaningful from a dolphin's perspective. Even the initial characterization of signals as whistles, click trains, and burst pulses can be problematic. Whistles and clicks may not be discrete categories either acoustically or physiologically, which suggests overlap of functions as well. Acoustically, whistles and click trains can be modeled to lie on opposite ends of a continuum relative to duty cycles (i.e., "the percentage of time that a signal is 'on' versus the total length of the signal") and inter-click or sinusoidal wave intervals, with burst pulses in the middle (Murray et al. 1998). Physiologically, the phonic lips in the nasal complex have a role in the production of both whistles and clicks (Cranford 2000; Au 2009). For some species, click trains and burst pulses are quantitatively different categories (Lammers et al. 2004); however, often no data are presented to justify the assumption that there is a quantitative difference between these broad categories.

Current knowledge suggests that whistles and burst pulses usually function in communication (Dudzinski et al. 2009) and that dolphins typically use click trains and click trains that grade into burst pulses for echolocation (similar to Madsen et al. 2005; DeRuiter et al. 2009). However, most research on delphinid signals has focused on whistles or echolocation clicks, and we know little about burst pulses and their functions. Burst pulses are of interest not only because they comprise a considerable portion of the repertoire of many dolphins (Janik 2009), but also because species from 6 odontocete families (including dusky dolphins) seldom or never whistle (Morisaka and Connor 2007), and instead likely use burst pulses for a wide range of communication purposes.

Characterizing burst pulses and click trains used by dusky dolphins are of particular interest, as an example of the repertoire of a (possibly) non-whistling delphinid.

Dusky dolphin signals have been described (see Au et al. 2010b for a summary), but past studies have focused only generally on whistles (although it is not clear if these are emitted by dusky dolphins), echolocation clicks, or echolocation behavior. The signal repertoire of dusky dolphins has not been characterized comprehensively, so the characterization presented here represents a unique opportunity to do so for a (possibly) non-whistling dolphin that exhibits coordination during foraging (Vaughn et al. 2010a). Studying how dusky dolphins use click trains and burst pulses to communicate and to coordinate foraging behaviors potentially provides insights into mechanisms of coordinated foraging. Dusky dolphins exhibit 2 broad foraging tactics: feeding at night on a deep scattering layer (e.g., in Kaikoura, Dahood and Benoit-Bird 2010) and feeding during the day in shallow bays on small schooling fishes (e.g., in Argentina and in the Marlborough Sounds, NZ; Vaughn et al. 2010a). They exhibit coordination during both tactics, and they often forming larger groups during foraging to contain or capture prey more effectively (Würsig and Würsig 1980; Pearson 2009)

Comparing signals between Argentina and NZ dusky dolphin populations provides an opportunity to increase our understanding of the repertoire of this semi-pelagic delphinid under different ecological conditions. In both locations, dusky dolphins at times coordinate behaviors to herd and capture schooling fish, and they feed with diverse associated predators including seabirds, pinnipeds, and sharks (Vaughn et al. 2007). In Argentina, dusky dolphins feed in much larger groups and for longer

durations (Würsig and Würsig 1980; Vaughn et al. 2007); these differences likely relate to differences in bay sizes and consequent sizes of fish schools (Vaughn et al. 2010a).

My objectives in this paper were to characterize dusky dolphin acoustic signals in Argentina and NZ and to compare signals between study sites relative to their categories, parameters, and proportions. I characterized signals by analyzing narrowband recordings made in Admiralty Bay and Current Basin, NZ, and Golfo Nuevo, Argentina (frequency ranges 0-16 kHz and 0-24 kHz, respectively). I determined how representative signals in these narrowband recordings were of signals in broadband recordings by comparing dusky dolphin signals from broadband recordings in Kaikoura, NZ (frequency range 0-200 kHz), to their counterparts in down-sampled narrowband recordings (frequency range 0-16 kHz).

Methods

Study sites

Dolphin signals were analyzed from Admiralty Bay (40°57'S, 173°55'E) and Current Basin (40°57'S, 173°48'E), NZ and Golfo Nuevo (42°40'S, 64°40W), Argentina. Admiralty Bay and Current Basin are located in the Marlborough Sounds region of NZ, where they are connected by French Pass. Golfo Nuevo is in the Patagonia region of Argentina. All three bays are relatively shallow, although Golfo Nuevo is much larger. Admiralty Bay and Current Basin depths are typically 30-50 m and 20-30 m, respectively while Golfo Nuevo depths are typically 40-100 m. Admiralty Bay is 160 km^2, Current Basin is 30 km^2, and Golfo Nuevo is 2500 km^2.

Data collection– NZ

Broadband recordings (0-200 kHz) of dusky dolphin signals were made in Kaikoura on 4 August 2006. Signals were recorded from a large group of approximately 150-200 dolphins exhibiting a combination of resting, traveling, and socializing behavior. These recordings were made from a Dolphin Encounters ecotourism boat (Buurman 2010) while swimmers were in the water. The hydrophone was lowered to a depth of 3 m from a stationary boat; the hydrophone was custom-built (by D Norris) and omnidirectional with a 20 dB pre-amplifier, a sensitivity of -190 dB re 1µPa, and a flat frequency response (+/- 3 dB) to approximately 170 kHz. The signal from the hydrophone was passed through a custom-built, signal conditioning electronics box where it was amplified by 46 dB and low-pass filtered at 150 kHz. Recordings were digitized using a PCI-DAS4020/12 analogue-to-digital converter sampling at a rate of 400 kHz. No other dolphin species were sighted in the group from which recordings were made, which indicates that recorded signals were from dusky dolphins.

I made narrowband recordings (0-16 kHz) of dusky dolphin signals in Admiralty Bay and Current Basin, from 5 August to 4 November 2005 and during August 2006. Signals were recorded while the dolphins were stationary and feeding during focal follows of dolphin groups. I collected data only when Beaufort sea states were ≤ 3, using a rigid-hulled inflatable boat with an 85 hp two-stroke (2005) or an 80 hp four-stroke (2006) Yamaha engine. I located dolphin groups by driving on predetermined transects or via opportunistic sightings. Once a group was located, I then conducted a focal follow on the group for up to 4 hrs, and recorded above-water behavioral data at 2

min intervals (for use in other studies, e.g., Vaughn et al. 2007, 2008, 2010b). When stationary feeding was observed, 1-2 researchers entered the water and recorded underwater video and acoustic data while swimming at the surface and occasionally doing shallow breath-hold diving. One observer documented underwater footage of feeding activity with a Sony DCR-HC1000 camcorder in an Amphibico™ housing equipped with a hydrophone, from which monaural audio data were later extracted. Audio data were collected with a sampling rate of 32 kHz and were generally recorded at a distance of 5-8 m from a prey ball. I examined recordings collected only on days when no other dolphin species were sighted, which reliably ensured that all analyzed data were dusky dolphin signals.

Data collection– Argentina

Narrowband recordings (0-24 kHz) of dusky dolphin signals were made in Golfo Nuevo during December 1998. Signals were recorded from groups exhibiting diverse behaviors (resting, socializing, traveling, and feeding). Recordings were made via surface swimming and shallow breath hold diving, using a manually operated mobile video/acoustic system with stereo hydrophones with a 48 kHz sample rate (Dudzinski et al. 1995). A 7 m boat was used as a research platform and more than one swimmer was typically in the water at one time, including (at times) SCUBA divers. Common dolphins (*Delphinus* spp.) were occasionally sighted with the focal dusky dolphin group. In my analyses, I did not examine signals that were recorded from groups that contained common dolphins, to ensure that analyzed signals were from dusky dolphins.

Criteria– selection of an individual signal

I used an individual signal as my unit of analysis. A signal was considered to be discrete if it visually was distinct from other signals, i.e., if transitions relative to ICIs, amplitude, and frequencies occurred along a gradient rather than abruptly, such that clicks appeared to comprise a single signal. If a gap of clicks occurred within a selection, the selection was considered to comprise one signal if no more than one click was missing in the gap, with the number of missing clicks counted from the side of the gap that had the smallest ICI; if 2 or more clicks were missing, the selection was considered to comprise two signals.

Comparison of signals in broadband recordings to their counterparts in down-sampled narrowband recordings

The duration of each broadband NZ acoustic file was approximately 10 s. To down-sample broadband Kaikoura recordings, I reduced the sampling rate from 400 kHz to 32 kHz, then saved the new file. I compared dusky dolphin signals in broadband recordings to their counterparts in down-sampled narrowband recordings by quantifying numbers and parameters. I used Adobe Audition 2.0 (1992-2005) to record start and end times of all signals that were visible in spectrograms (resolution = 512 points, windowing function = Blackmann-Harris). Matlab 2009b (version 7.9.0.529, MathWorks™) was used to apply a signal processing algorithm written by Lammers et al. (2004) to quantify parameters for non-overlapping signals that had a good signal-to-noise ratio. For these signals, I calculated repetition rate, ICIs, duty cycles, center frequencies, and 3-dB bandwidths.

I quantified repetition rates, ICIs, and duty cycles for comparison between narrowband and broadband data. ICI is the duration of time between subsequent clicks. Duty cycle is "the percentage of time that a signal is 'on' versus the total length of the signal" (Murray et al. 1998), and is a measure of the degree to which a signal is tonal or pulsed. I also examined the center frequency and 3-dB bandwidth of individual clicks because they are robust to high levels of ambient noise, varying distances of the dolphin to the camera, and varying head orientations towards the camera. Center frequency is the frequency that separates the spectrum of the signal into two parts with equal energy (Charif et al. 2008). The 3-dB bandwidth represents the frequency bandwidth around the center frequency where the signal is decreased by 3 dB (Crane and Lashkari 1996).

Narrowband recordings: signal measurements

To analyze signals in NZ narrowband recordings, video files were divided into 2-min segments to correspond to above-water data that were collected concurrently. Mono audio files were examined using Adobe Audition, and then organized according to subjective signal-to-noise quality (high, medium, or low). From documented start and end times, durations were calculated for all high and medium quality signals with a minimum peak A/D sample value ≥ 1000 on a 16 bit scale between 32,767 and -32,768. Matlab was used to quantify additional parameters for only signals with a sample value ≥ 1000 that had a good signal-to-noise ratio and did not overlap another signal.

To analyze signals in Argentina narrowband recordings, for each 2-channel audio file, data from only one channel were examined: the channel that recorded the highest quality signals. Adobe Audition was used to record start and end times for all visible

signals from which durations were calculated. I used Matlab to quantify additional parameters for non-overlapping signals, according to the same criteria described above. Median duration of Argentina narrowband acoustic files that we analyzed was 7 s (IQR = 5-10, range = 3-17).

Statistical analyses

For statistical analyses, I used SPSS 13.0 for Mac (SPSS Inc., Chicago, IL). Central tendencies for acoustics parameters are presented as means ± standard deviations. I used independent sample t-tests (IS t-test) and one-way ANOVAs with Bonferroni post hoc corrections to test for differences between groups. For ANOVA comparisons, when variances differed between groups, I used a Brown-Forsythe test to determine group differences. I used paired sample t-tests (PS t-test) to compare broadband signals to their down-sampled narrowband counterparts and Pearson's correlations (PC) to examine relationships between variables.

Results

Broadband recordings– NZ

I identified 733 signals from NZ broadband recordings. Of these, 189 (26%) were also present in the down-sampled narrowband recordings. There were differences between signals that extended below 16 kHz and those that did not. Signals that extended below 16 kHz had shorter durations ($t = -8.645$. $P < 0.001$), a higher repetition rate ($t = 2.318$, $P = 0.027$), shorter ICIs ($t = -7.877$, $P < 0.001$), larger duty cycle values ($t = 3.191$, $P = 0.002$), lower center frequencies ($t = -15.619$, $P < 0.001$), and smaller 3-

dB bandwidths (t = -7.016, $P < 0.001$) than signals that did not extend below 16 kHz (IS t-tests) (Figure 13).

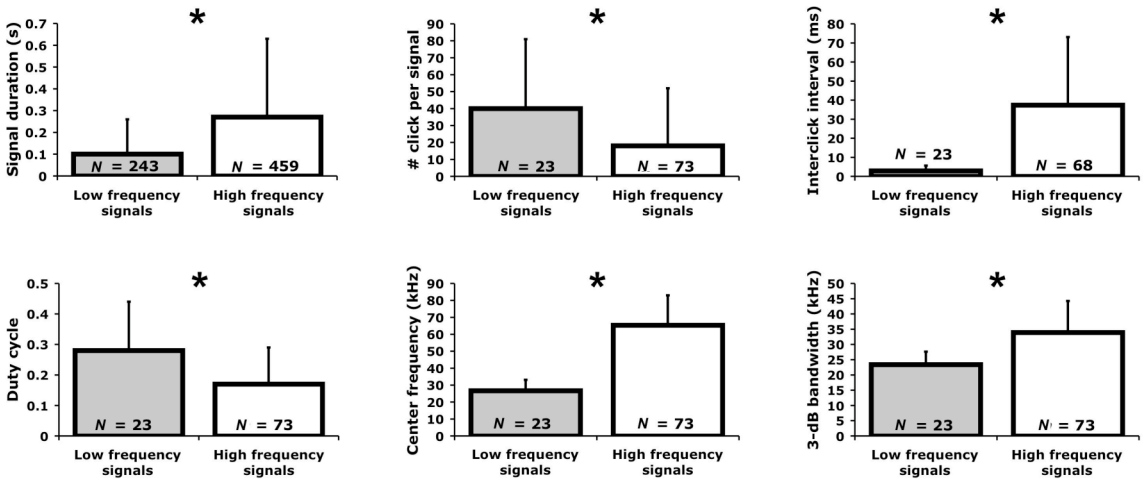

Figure 13. A comparison of mean parameters between signals in broadband recordings that extended into low frequencies (< 16 kHz), and signals that did not. Error bars show standard deviations, and * indicates significant differences via independent samples t-tests.

For signals that extended below 16 kHz, signals in broadband recordings did not differ from their down-sampled narrowband counterparts in repetition rates (t = -1.838, $P = 0.08$) or ICIs (t = 0.010, $P = 0.992$). However, signals did differ in durations (t = -12.509, $P < 0.001$) and duty cycles (t = -9.672, $P < 0.001$) (PS t-tests, n = 23). Signals in broadband recordings had shorter durations (mean difference = 0.01 ± 0.004 s) and smaller duty cycle values (mean difference = 0.44 ± 0.22) than did their counterparts in down-sampled narrowband recordings. Down-sampling broadband signals added error

to duty cycle values, and the signal differences between broadband and down-sampled narrowband recordings were not simply linear (PC: $R^2 = 0.0191$, $N = 23$).

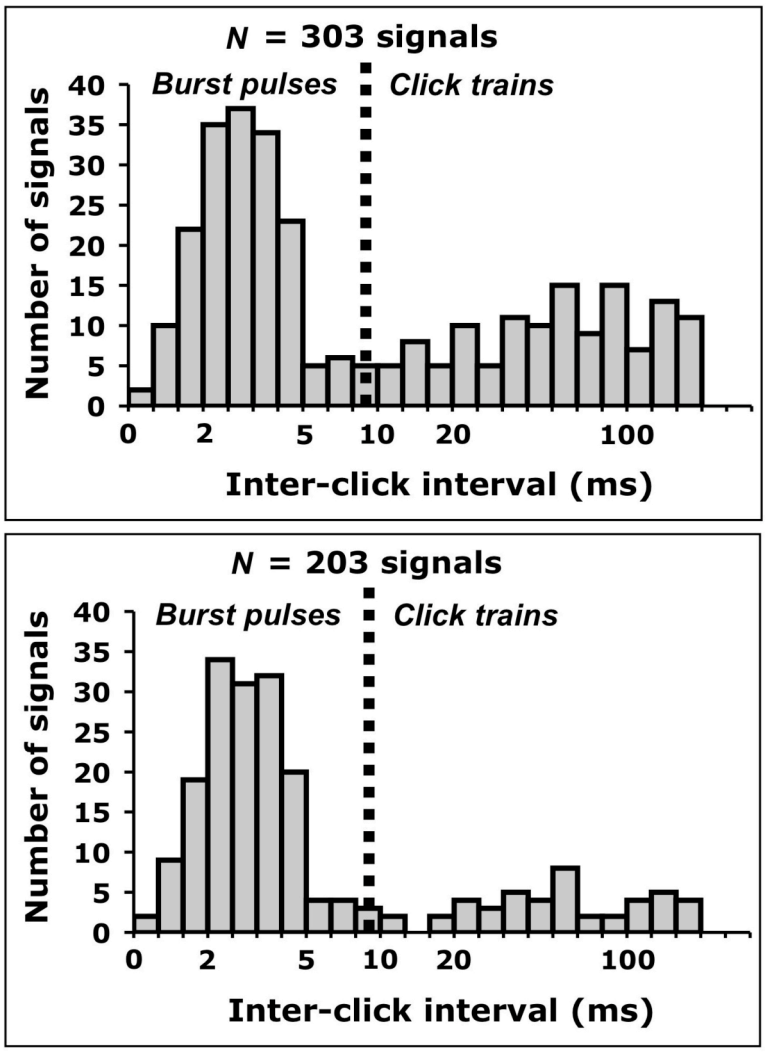

Figure 14. From NZ narrowband recordings, histograms of mean ICIs for all signals (top), and for only those signals that had a constant ICI (bottom). X-axis is on a logarithmic scale.

Narrowband recordings– NZ

I identified 2,285 signals from 22 feeding bouts in narrowband NZ recordings. I analyzed 314 of these in Matlab; I was unable to analyze the rest because they overlapped another signal or did not have a good signal-to-noise ratio. Since the previous results indicated that only ICIs were robustly consistent between broadband and down-sampled narrowband signals, I used this parameter to categorize signals in narrowband recordings. The distribution of ICIs of these signals was bimodal (Figure 14). Although it was difficult to determine the exact division point between the two modes, the division was approximately at 9.25 ms, or the ICI that separates click trains from burst pulses.

Because of this bimodal ICI distribution, I initially categorized all signals as click trains, burst pulses, or click train-burst pulse combinations, from spectrograms (Figure 15). Of 2,285 total signals, 43% were click trains, 39% were burst pulses, and 18% contained click train-burst pulse components; Table 5 shows direction of ICI changes during these signals. Click trains, burst pulses, and click train-burst pulse combinations differed in duration (ANOVA: $P < 0.001$) (Table 6): burst pulses had shorter durations than click trains ($P < 0.001$) and click train-burst pulse combinations ($P = 0.001$). Click trains had shorter durations than click train-burst pulse signals ($P < 0.001$).

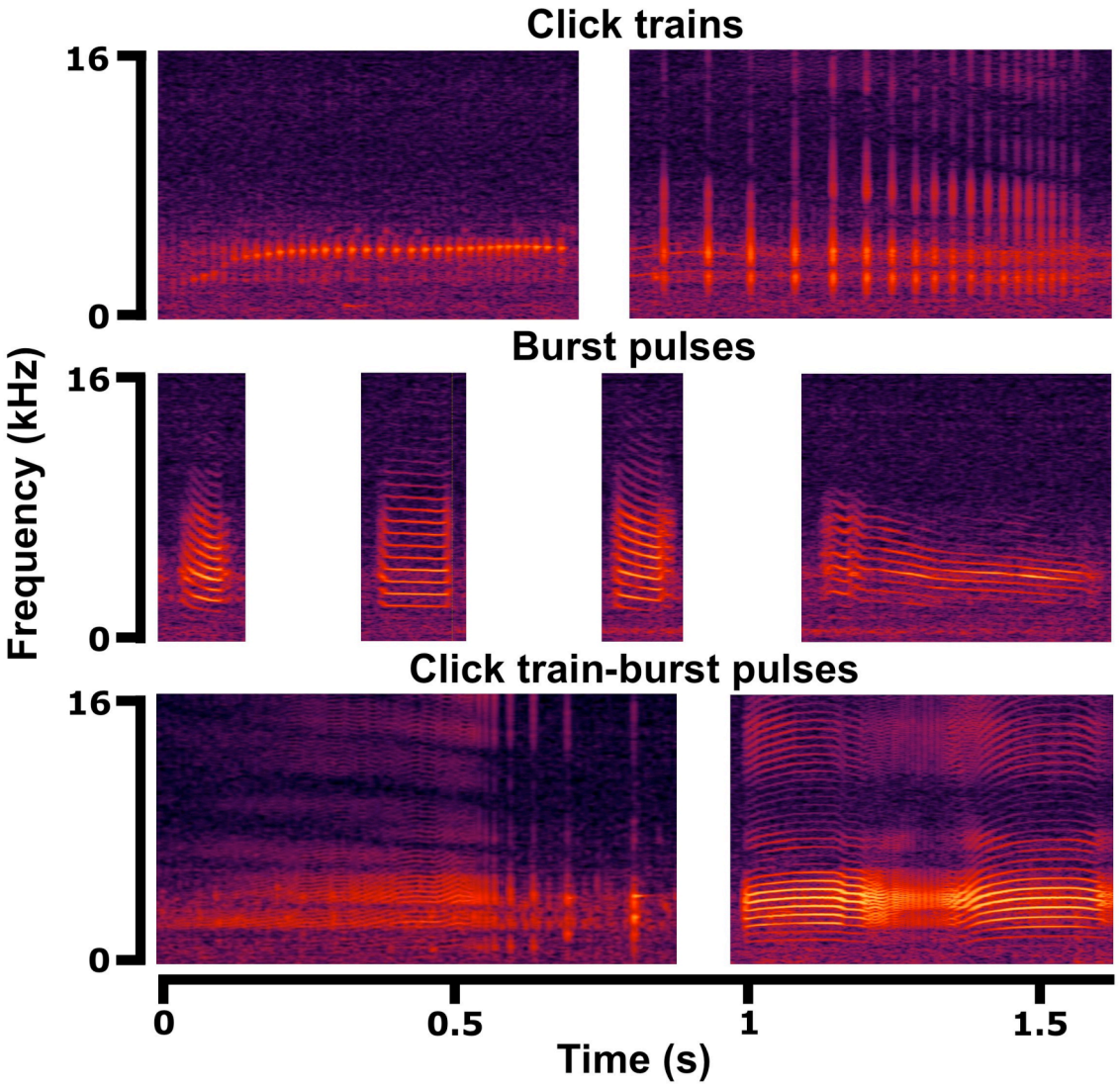

Figure 15. Spectrogram examples of each signal category, from NZ narrowband recordings.

Table 5. From narrowband recordings, percentage of each signal category that presented constant ICIs, had decreasing ICIs, had increasing ICIs, or had ICIs that changed in both directions during the signal. $N = 2{,}285$ signals in NZ; $N = 335$ signals in Argentina. NA = not applicable.

	Constant	**Decreasing**	**Increasing**	**Both directions**
Click trains				
NZ	30%	20%	30%	20%
Argentina	60.5%	15%	13%	11.5%
Burst pulses				
NZ	71%	24%	4%	1%
Argentina	97%	1%	1%	1%
Click train-burst pulse combinations				
NZ	NA	39%	24%	37%
Argentina	NA	48%	13%	39%

Table 6. Signal durations (s) from narrowband recordings. SD = standard deviation.

	Mean	**SD**	**min**	**max**	**# signals**
Click trains					
NZ	0.75	0.76	0.01	8.70	961
Argentina	0.51	0.55	0.003	2.96	92
Burst pulses					
NZ	0.31	0.33	0.001	1.79	886
Argentina	0.10	0.16	0.01	1.27	214
Click train-burst pulses					
NZ	1.09	0.67	0.02	3.53	416
Argentina	0.76	0.72	0.04	2.32	22

I observed no whistles in narrowband recordings, but I did observe 3 chirp-scream burst pulses (0.3% of burst pulses, Figure 16). All chirp-screams occurred during a single, very high-activity feeding bout. Chirp-screams differed from other burst pulses in that they had very short ICIs (0.32 ms and 0.53 ms for the 2 analyzable examples, the next highest ICI was 1.16 ms). They also had low center frequencies (4.77 kHz and 4.48 kHz) and small 3-dB bandwidths (4.45 kHz and 4.53 kHz). They appeared to occur only at narrowband frequencies.

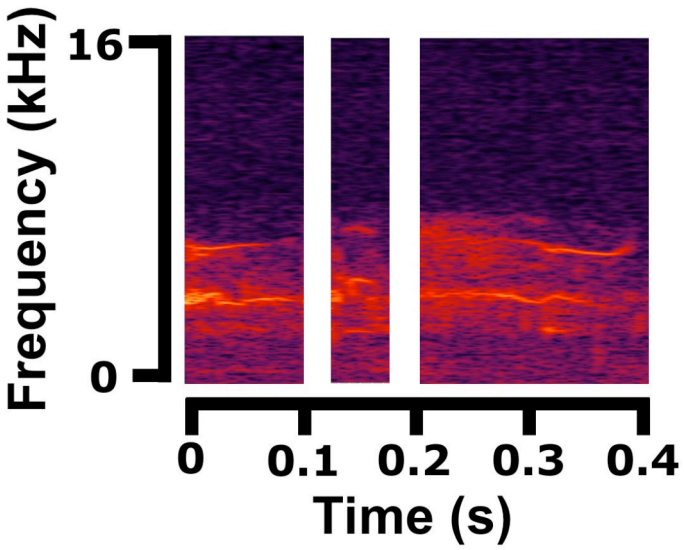

Figure 16. Spectrograms for the 3 chirp-screams that were present in NZ narrowband recordings.

In addition to the above 4 categories of single signals, I observed sequences of 2 or more consecutive burst pulses that occurred within 0.2 s, and visually and aurally appeared closely matched (Figure 17, see below for quantitative details). Of 886 burst

pulses, 610 (69%) occurred within 0.2 s of another burst pulse; 543 of these burst pulses occurred within 0.2 s of another burst pulse with which it did not overlap (61% of all burst pulses). Burst pulses that occurred > 0.2 s apart from each other did not visually or aurally match. Of non-overlapping burst pulses that occurred within 0.2 s of another burst pulse, 372 (69 %) occurred in a burst pulse sequence. Thus, 42% of all burst pulses occurred in sequences.

In total, I observed 147 burst pulse sequences. Most sequences consisted of burst pulse combinations that were observed infrequently or only once (similar to Rankin et al. 2007; Figure 17a, b, and c). However, one sequence category consisted of a possibly stereotyped short-long burst pulse combination that was observed frequently (Figure 17d). Within each sequence, I compared burst pulse parameters to quantify similarity. I determined the maximum difference between burst pulses within a sequence, and then used this maximum to calculate the mean maximum difference across all sequences. For all sequences, maximum intra-sequence difference in ICI was 1.00 ± 0.49 ms (range = 0-2.00 ms, $N = 31$ sequences), difference in center frequency was 0.30 ± 0.22 kHz (range = 0.057-0.94 kHz, $N = 31$), and difference in 3-dB bandwidth was 0.55 ± 0.47 kHz (range = 0.005-1.80 kHz, $N = 31$).

Of the 147 burst pulse sequences, 108 (73.5%) occurred infrequently or only once, 28 (19%) were stereotyped short-long sequences, and 11 (7.5%) were longer sequences that contained stereotyped short-long portions. For sequences that occurred infrequently or only once, the majority (65%) contained 2 burst pulses. A smaller percentage of these sequences were more complex: 27% of these sequences contained 3,

6% contained 4, 2% contained 6, and 1% contained 7 burst pulses. For sequences that contained stereotyped short-long portions, 36% contained 3, 36% contained 4, and 27% contained 6 burst pulses.

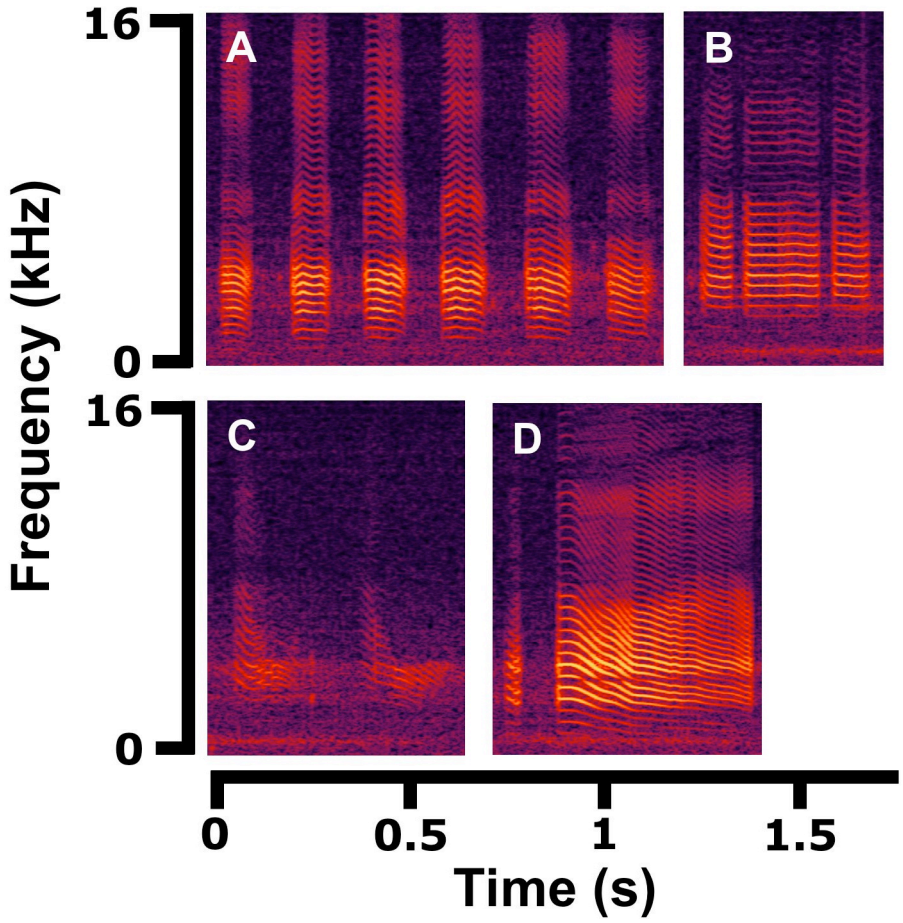

Figure 17. Spectrogram examples of sequences of burst pulses. Sequences consisted of burst pulse combinations that were observed only one time or infrequently (a, b, c), and a short-long burst pulse combination that was observed frequently (d).

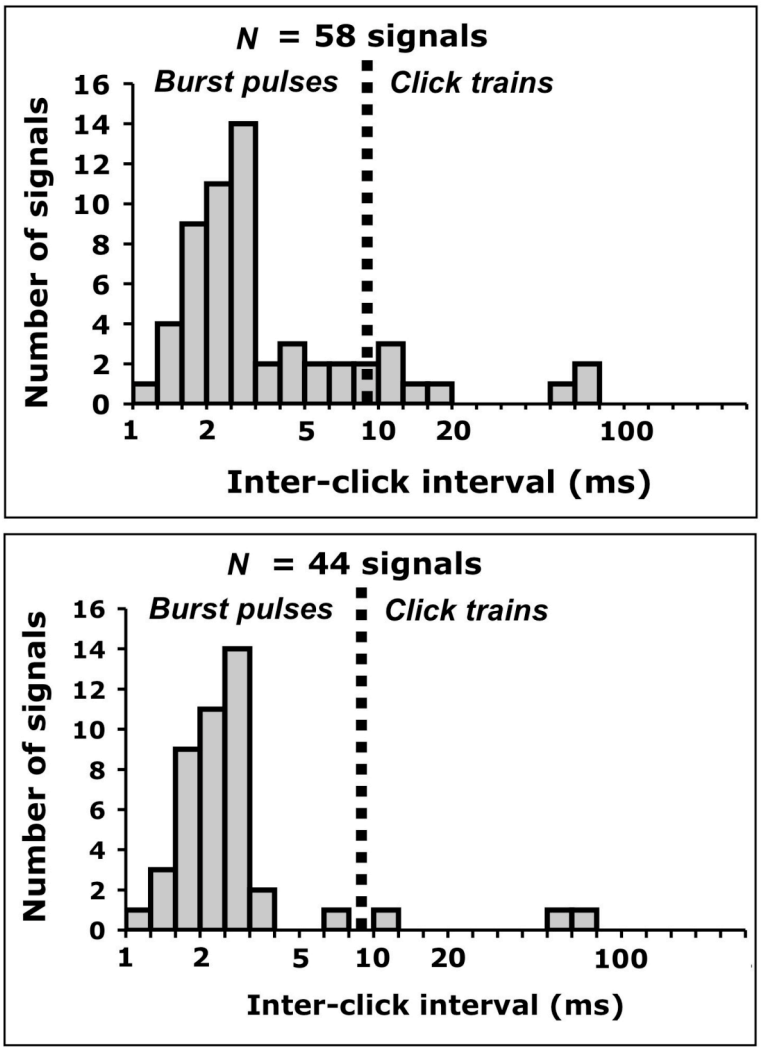

Figure 18. From Argentina narrowband recordings, histograms of mean ICIs for all signals (top), and for only those signals that had a constant ICI (bottom). X-axis is on a logarithmic scale.

Narrowband recordings– Argentina

From Argentina recordings, I analyzed 341 signals from 2 groups on 2 days; I analyzed 59 of these in Matlab. Distributions of ICIs were unimodal and centered on signals with burst pulse intervals (Figure 18). To be consistent with NZ signal

categories, I used spectrograms to categorize Argentine signals as click trains, burst pulses, or click train-burst pulses. A click train was defined as clicks with a spacing of at least 9.25 ms. Of 335 total signals, 29% were click trains, 64% were burst pulses, and 7% were click train-burst pulse combinations; Table 5 shows direction of ICI changes during these signals. Click trains, burst pulses, and click train-burst pulses differed in durations (ANOVA: $P < 0.001$) (Table 6). Burst pulses had shorter durations than click trains ($P < 0.001$) and click train-burst pulse combinations ($P < 0.001$). Click trains had shorter durations than click train-burst pulses ($P = 0.009$).

I observed no chirp-scream burst pulses within Argentine recordings; however, we observed 38 sequences of burst pulses. Of 215 burst pulses, 188 (87%) occurred within 0.2 s of another burst pulse; 185 occurred within 0.2 s of another burst pulse with which it did not overlap (86% of all burst pulses). Of non-overlapping burst pulses that occurred within 0.2 s of another burst pulse, 138 (75%) occurred in a burst pulse sequence. Thus, 64% of all burst pulses occurred in sequences. Of the 38 burst pulse sequences, 31 (81.5%) occurred infrequently or only once, 4 (10.5%) were similar to the stereotyped short-long sequence that occurred in NZ, and 3 (8%) were longer sequences that contained the stereotyped short-long burst pulses. No other stereotyped sequences were observed. I was not able to compare burst pulse parameters within and between sequences because of the small sample size. For sequences that occurred infrequently or only once, 42% contained 2, 13% contained 3, 19.5% contained 4, 13% contained 5, 6% contained 6, 3.25% contained 9, and 3.25% contained 14 burst pulses. For sequences

that contained stereotyped short-long burst pulse portions, 67% contained 3, and 33% contained 6 burst pulses.

Discussion

Broadband signals– NZ

Parameter differences between click signals that extended below 16 kHz and those that did not suggest that dusky dolphins may use click signals of different frequencies for different purposes. Low frequency signals had shorter durations, but they contained more clicks that were spaced much more closely together than high frequency signals. Delphinids typically use brief but rapid burst pulses of sound for communication (Janik 2009), whereas they use longer duration widely spaced click trains for echolocation (Frankel 2009). Dusky dolphins may similarly use low frequency burst pulses of sound for communication, and high frequency widely spaced clicks for echolocation. Additionally, low frequency signals were characterized by larger duty cycle values, which means that they were more tonal. Delphinids typically use whistles and burst pulses for communication (Dudzinski et al. 2009; Janik 2009), both of which have have larger duty cycle values than do click trains (Murray et al. 1998), so this pattern is also consistent with a likely communication function for low frequency dusky dolphin signals. Alternatively, it is possible that the differences between high and low frequency dusky dolphin signals may be due to differences in the dolphin's orientation or distance to the hydrophone (Au 2009).

There are a number of potential benefits to using lower frequency signals for communication. They travel farther underwater than do higher frequency signals (Tyack

1998), increasing communication distance. Additionally, it may require less energy to produce lower frequency signals. If this is the case, then when it is not beneficial for dolphins to produce a broadband signal for echolocation, they may instead use a low frequency signal (i.e., for communication). However, there may be costs of using low frequency signals for communication, including the ability of predators such as killer whales to hear those frequencies (Morisaka and Connor 2007) and potential eavesdropping by more distant dolphins (similar to Janik 2000a; Gregg et al. 2007), depending on the source level of the signal.

Similarities between NZ and Argentina signals in narrowband recordings

The most robust signal measurement parameter between broadband and narrowband recordings was ICIs, so I used this parameter to categorize signals in narrowband recordings. ICIs of signals in narrowband recordings had a bimodal distribution in NZ, which indicates that click trains (with long inter-click intervals) and burst pulses (with short ICIs) were quantitatively distinct categories for dusky dolphins. A similar quantitative difference was found between the ICIs of click signals of spinner dolphins in Hawaii (Lammers et al. 2004), which suggests that delphinids in general may use click trains and burst pulses for different purposes. Click trains appear to most often be used for echolocation (Frankel 2009), while burst pulses appear to most often be used for communication (Dudzinski et al. 2009; Janik 2009). In Argentina, ICI distributions were unimodal and centered on burst pulses; however, we were only able to analyze a small number of click trains. It is possible that a larger sample size would reveal a bimodal ICI distribution with a second mode centered on click trains.

The 4 main signal categories that I observed were click trains, regular burst pulses, click train-burst pulse combinations, and chirp-scream burst pulses. The former 3 categories were quantitatively determined, while the latter category was qualitatively assessed. Individual click trains and individual burst pulses were commonly recorded, but signals that contained both click train and burst pulse components were recorded less often. Signals in which a click train turns into a burst pulse (i.e., a "terminal buzz") often are used by other odontocetes in a prey-capture function (e.g., Blainsville's beaked whales, *Mesoplodon densirostris*, Madsen et al. 2005; harbour porpoises, *Phocoena phocoena*, DeRuiter et al. 2009; sperm whales, *Physeter macrocephalus*, Miller et al. 2004). I observed this category infrequently in this study; this might be because, if dusky dolphins use a terminal buzz when they attempt a prey-capture it may be of higher frequency. One might indeed expect a higher frequency terminal buzz to be used given the small size of the fish that dusky dolphins eat (about 6-15 cm, Würsig and Würsig 1980), since higher frequency sounds are more directional (Tyack 1999).

ICI direction frequently changed during a single signal, but the prevalence of each direction change (constant, increasing, decreasing, or changing in both directions) was similar among click trains and click train-burst pulses. In contrast, burst pulses were much more likely to have constant ICIs than they were to have ICIs that changed. Burst pulses may be more likely to have constant ICIs because they have shorter durations than do click trains and click train-burst pulses. Both their constant ICIs and their short durations suggest that burst pulses have a role in communication (Dudzinski et al. 2009; Janik 2009), in contrast to the frequent echolocation role of click trains or

combination click train-burst pulses (DeRuiter et al. 2009; Akamatsu et al. 2010), which often requires varying ICIs according to distance to the object of echolocation (Madsen et al. 2005; Frankel et al. 2009).

Whistles are used for communication by many odontocetes (Dudzinski et al. 2009; Janik 2009); however, I recorded no whistles in our narrowband NZ recordings. The 3 chirp-screams that we recorded in NZ were whistle-like and consisted of very closely spaced clicks that appeared to be concentrated at low frequencies (about 4-5 kHz). Chirp-screams were recorded during a very active feeding bout, which suggests that they may be used for social communication, or during times of excitement. I was unable to determine which dolphins produced which signals; however, one chirp-scream occurred at the exact time that 2 dolphins doing socio-sexual behaviors swam close to the videocamera. For other dolphins in the wild, screams have been associated with aggressive behavior (Herzing 1996), play or other social behaviors (Dudzinski 1996), and excited behaviors (Dudzinski 1996). Chirps have been associated with play or with individuals approaching each other after being separated (Dudzinski 1996)

In addition to these 4 main categories, I also observed sequences of burst pulses at both study sites, which were comprised of individual burst pulses that visually and aurally were closely matched. These sequences were common: 42% of burst pulses in NZ compared and 64% of burst pulses in Argentina occurred in sequences that contained 2-14 burst pulses. The diversity in the number of burst pulses that made up sequences and in burst pulse parameters suggest that these sequences functioned in communication. Burst pulses may have communication functions not just in their individual content, but

also in the repetition of pulses or of particular burst pulse combinations. Sequences of killer whale calls occurred in British Columbia (Riesch et al. 2008), and these often occurred during close-range interactions between individuals (Riesch et al. 2008). Stereotyped and repeated sequences of burst pulses occurred in northern right whale dolphins (*Lissodelphis borealis*, Rankin et al. 2007), and it was suggested that these sequences played a communicative role that is similar to stereotyped whistles (e.g., individual or group identification, Rankin et al. 2007). For dusky dolphin burst pulse sequences, it seems unlikely that they functioned in individual or group identification, since only one sequence category was repeated frequently.

Differences between NZ and Argentina signals in narrowband recordings

Sample sizes were larger in NZ than in Argentina, and dolphin behaviors were different between sites. Behavioral differences likely accounted for acoustic differences between sites, although sample size or social learning might have had a role in acoustic differences (Janik and Slater 2000). In Argentina, a smaller percentage of signals were click trains (29% versus 43% in NZ), and click train-burst pulses (7% versus 18% in NZ), and click trains more often had constant ICIs. These acoustic differences were likely due to behavioral differences between study sites. Dusky dolphins in NZ may have used click trains and click train-burst pulses more often because they were engaged in foraging during recordings. Additionally, they may have changed click train ICIs to a greater extent because they were using these clicks for foraging-related echolocation such as approaching prey for capture. In contrast, Argentina dusky dolphins may have been more likely to use click trains with constant ICIs because they used these clicks for

non-foraging functions such as navigating their environment or surveying it for predators.

In Argentina, a greater percentage of signals were burst pulses (64% versus 39% in NZ), a greater percentage of burst pulses occurred in sequences (64% versus 42% in NZ), and sequences contained more burst pulses (up to 14 in Argentina versus up to 7 in NZ). Argentine dolphins likely produced more burst pulse and sequences, and used more complex sequences, because they were engaging in social behaviors during many of the recordings, whereas NZ dolphins seldom displayed social behaviors during recordings. Alternatively, it is possible that differences between sites in social learning may have led to long-term differences in how dusky dolphins at each site use signals. Argentine dusky dolphins may use more burst pulses and sequences, and more complex sequences, to allow large groups of dolphins to effectively communicate during coordinated foraging (Würsig and Würsig 1980; Degrati et al. 2008). While dusky dolphins in NZ also coordinate a great deal during foraging, they do so in smaller groups (Vaughn et al. 2007, 2010a).

How did ecology versus social learning relate to acoustic signals?

Overall, ecology related to acoustic signals on a broad scale, while cultural differences were evident on a finer scale. Broad similarities between locations suggest that general ecological context related to broad signal categories and parameters, and likely also functions of signals. Signals at each location were categorized as click trains, burst pulses, or click train-burst pulses, and two unique burst pulse variations were observed: chirp-screams (observed only in NZ) and sequences of burst pulses (observed

at both locations). Parameter differences between and within locations suggest that burst pulses including chirp-screams and sequences were likely used for communication, while click train-burst pulses were used for echolocation. The function of low frequency click trains was unclear, but likely relates to foraging in some capacity (e.g., echolocation, communication, or containing prey). One might expect cultural differences to be evident on a finer scale, such as in categories of burst pulses used for communication. One example of these fine scale differences may be the marked difference between study sites in number of burst pulses present in sequences, in that Argentina sequences contained up to twice as many burst pulses as did NZ sequences. Broad acoustic signal categories and functions likely are adaptive for navigating in temperate Continental Shelf habitats, foraging on schooling fishes and a deep scattering layer, and communicating within a fission-fusion social structure. Fine-scale differences in acoustic signals between locations may be a result of long-term learning specific to the ecological context of each location.

CHAPTER V

DUSKY DOLPHIN SIGNALS: FUNCTIONS DURING BAIT-BALLING OFF NEW ZEALAND

Introduction

Vertebrate acoustic signals have diverse functions in marine environments, and these signals have evolved to adapt vertebrates to a habitat with limited visibility and unique sound propagation properties (Wartzok and Ketten 1999). Since visibility is often limited, acoustic signals are particularly effective for communication (Dudzinski et al. 2009; Janik 2009). Saltwater characteristics make it possible for sound to travel long distances, particularly through ocean sound channels, which enables long distance communication (Clark 1990; Tyack 1999). For example, low frequency signals used by fin and blue (*Balaenoptera musculus*) whales could travel thousands of kilometers in pre-shipping days (Payne and Webb 1971), and blue whale signals have been recorded at a distance of 400-600 km in current ocean conditions (Stafford et al. 1998). Some odontocetes also use echolocation signals to gather information about their environment, both at distance and at close range (Madsen et al. 2005, Akamatsu et al. 2010). Echolocation allows odontocetes to forage effectively in diverse habitats including at depth, in murky waters, at times under the sand, and at nighttime. Additionally, odontocetes potentially use signals to manipulate or contain prey, which may facilitate prey capture or prevent prey from escaping.

Although delphinids use diverse modalities to communicate including visual, tactile, and chemical, they most often communicate acoustically (Dudzinski et al. 2009; Janik 2009). In a foraging context, dolphin communication can facilitate coordination of behaviors, "call" other dolphins to a feeding bout to help contain a prey ball, or merely be excited social banter. Dolphins may coordinate behaviors so that they are better able to contain a prey ball or to capture prey (Würsig and Würsig 1980; Similä & Ugarte 1993; Gazda et al. 2005). At other times, coordination of behaviors may function in helping dolphins to alternate which dolphin approaches the prey ball for a prey-capture attempt. "Calling" other dolphins to a feeding bout can be intentional or unintentional. For dusky dolphins off Argentina, it was hypothesized that individuals did noisy leaps to call others to a feeding bout by hearing the sound underwater but also by sight of the leap in-air (Würsig 1986), so that the group was able to contain a prey ball at the surface. For bottlenose dolphins in the Moray Firth, Scotland, low frequency brays have the effect of attracting other dolphins to the feeding area (Janik 2000a). However, these calls appear to be simply a byproduct of feeding and likely do not intentionally attract other dolphins. Social banter likely also occurs during feeding, at least to some degree. In Admiralty Bay, NZ, feeding behaviors are at times interspersed with social behaviors (R Vaughn, unpublished data, 2005-2006); it would make sense that feeding-related signals are similarly interspersed with other signals.

Dolphins use echolocation to determine presence and characteristics of objects in their environment, including conspecifics, prey, and predators. In a foraging context, dolphins and other odontocetes use echolocation to locate prey at a distance (Tyack

1999), and also to target individual prey items at close range during prey-capture attempts (Madsen et al. 2005; Akamatsu et al. 2010). One benefit of foraging in groups is that each individual may echolocate less often, either due to eavesdropping (Gregg et al. 2007) or cooperation (Würsig 1986).

Delphinids may also use acoustic signals to contain prey or to manipulate prey just prior to a prey-capture attempt. Schooling fishes tend to either exhibit escape behaviors when they hear dolphin signals (Wilson and Dill 2002; Doksaeter et al. 2009), or to cluster together more tightly (Nøttestad and Axelsen 1999). The former behavior provides an opportunity for dolphins to use signals to contain fish (similar to humpback whale bubble feeding, Jurasz and Jurasz 1979) while the latter behavior allows dolphins to use signals to increase the effectiveness of prey-capture behaviors. For example, killer whales off Norway do tail slaps to stun fish to make it easier to capture them (Simon et al. 2006). They emit low frequency signals just prior to doing tail slaps, which cause schools of herring to bunch together more tightly such that more fish are stunned (Simon et al. 2006). Other dolphins may emit signals of high intensity that stun or disorient fish, thus making them easier to capture (Norris and Møhl 1983). However, it is unclear if the signals emitted by dolphins are of sufficient intensity to have this effect on schooling fish (Benoit-Bird et al. 2006).

Among odontocetes, different categories of acoustic signals are used for different behavioral purposes. Categories that are most often are used for communication are whistles and burst pulses (Janik 2009). Categories that are most often used for click trains and those that grade into burst pulses (Madsen et al. 2005; Akamatsu et al. 2010).

However, signal functions can also fall outside of these broad generalizations; e.g., click trains may also function in communication (Janik 2009; Clausen et al. 2010). Currently, we understand little about specific burst pulse functions (e.g., as social chatter, to facilitate coordinated foraging, or to call other dolphins to a feeding bout), or specific echolocation roles (e.g., to stay alert to potential predators, or to locate or localize prey). And, we know little about if, or how, dolphins use signals to contain or herd prey, or to facilitate capturing prey, although beaked (Madsen et al. 2005) and sperm (Miller et al. 2004) whale emit feeding buzzes just before a prey capture that may have this effect. Dusky dolphins are a good species for examining function of acoustic signals during foraging. They exhibit a broad behavioral repertoire in their foraging behavior including coordination, which suggests complexity in their use of signals. They seldom if ever whistle, so examining these signals provides an opportunity to study communicative click train and burst pulse functions.

Dusky dolphins are distributed in the southern hemisphere over and near the continental shelf off South America, NZ, and southwestern Africa (Würsig et al. 2007). They forage using 2 general tactics, which are habitat-specific. Where a deep scattering layer occurs (e.g., off Kaikoura, NZ), dusky dolphins primarily feed at night, when the layer is closest to the surface (Dahood and Benoit-Bird 2010). Over the continental shelf (e.g., in Admiralty Bay, NZ and off Argentina), they feed during the day on small schooling fishes, mainly from the Order Clupeiformes (Vaughn et al. 2010a). This study occurred during 2005 and 2006, in Admiralty Bay and Current Basin, NZ, in the Marlborough Sounds region. Here, dusky dolphins may coordinate behaviors to herd

and capture schooling fish, and they feed with other predators including seabirds, pinnipeds, and sharks (Vaughn et al. 2007). During feeding bouts in 2005 and 2006, dolphin group sizes ranged from 1 to 30 individuals, prey ball sizes ranged from 0.5-32.5 m^2 on the side of the prey ball, and feeding durations ranged from 1 to 42 min (Vaughn et al. 2007).

My objectives were to investigate function (s) of dusky dolphin signals during foraging by relating group behavioral parameters to signal numbers and durations. I examined how signals functioned in communication by relating them to dolphin group sizes and degree of coordination during feeding. I assessed how they functioned in prey captures by correlating them to number of prey-capture attempts per dolphin per feeding interval. I determined how they functioned in prey herding by relating them to prey ball sizes, since larger prey balls appear to be more difficult for dolphins to contain (Vaughn et al. 2010b); and by relating signal parameters to number of herding behaviors per dolphin per feeding interval. Finally, I described changes in signal parameters that occurred during the course of a feeding bout.

Methods

Study sites

Dusky dolphin behaviors and acoustic signals were analyzed from Admiralty Bay (40°57'S, 173°55'E) and Current Basin (40°57'S, 173°48'E), NZ. These adjacent bays are located in the Marlborough Sounds region of NZ. Typical depths of Admiralty Bay and Current Basin are 30-50 m and 20-30 m, respectively; their areas are 160 km^2 and 30 km^2, respectively. Water clarity in Admiralty Bay and Current Basin during the

2005 and 2006 study seasons was a mean of 10 m ± 3 SD (range = 5-18 m measured using a Secchi disk, Vaughn et al. 2010b).

Data collection

I recorded data from 5 August to 4 November, 2005 and during all of August, 2006, from a rigid hulled inflatable boat with an 85 hp two-stroke (2005) or an 80 hp four-stroke (2006) Yamaha engine. I collected data only when the Beaufort sea state was ≤ 3. Dolphin groups were located on predetermined transects and via opportunistic sightings. A focal follow was then conducted on the group for up to 4 h, during which above-water data were recorded at 2-min intervals. I recorded above-water data on group size, location, and predominant behavior.

I determined group size by including all dolphins that were at a maximum distance of 10 m from another dolphin in the group (Smolker et al. 1992). I calculated dolphin group sizes for each 2-min feeding interval as the median number of dolphins present at the start and end of an interval. Predominant behavior was considered to be the behavior exhibited by most of the group for most of the 2-min interval. Feeding was defined as high-level activity that changed direction frequently and that included burst swims or leaping. Above-water dolphin data were recorded by one observer, while following the group at a distance of 25-50 m.

During stationary dolphin feeding, one observer recorded underwater video footage while snorkeling. Data were typically recorded 5-8 m distant from the prey ball. Underwater video footage of feeding activity was recorded using a Sony DCR-HC1000 videocamera in an Amphibico housing, from which single-hydrophone audio data were

later extracted. The videocamera recorded audio data with a sampling rate of 32kHz. I analyzed recordings only on days when I observed no other dolphin species in Admiralty Bay or Current Basin. Underwater video footage was synchronized in time with above-water follow data.

Acoustic analyses

To compare signal numbers and durations to dolphin group and prey ball sizes, I analyzed acoustic files as 2-min segments that corresponded to above-water dolphin group size and underwater prey ball size data. I used Adobe Audition version 2.0 (1992-2005) to divide video files into 2-min sections, and then to extract acoustic files from the video files. I organized acoustic files by quality (high, medium, or low) according to signal-to-noise ratio and analyzed only those files that contained high or medium quality signals. To compare signal numbers and parameters to prey herding and capturing parameters, I subsequently divided 2-min acoustic files into 1-min files to correspond to the portion of the underwater video behavioral dataset for which I was able to quantify herding and prey-capture behaviors (see below).

For these 2-min and 1-min acoustic files, I recorded start and end times for all signals that had a minimum peak A/D sample value ≥ 1000 on a 16 bit scale between 32,767 and -32,768, and these signals were categorized using spectrograms (sampling rate = 32 kHz, resolution = 512 points, windowing function = Blackmann-Harris). I categorized each signal according to previously determined quantitatively discrete categories (Chapter IV), as a click train, regular burst pulse, chirp-scream burst pulse, or click train-burst pulse combination. A click train was defined as a broadband signal with

an inter-click interval (ICI) ≥ 9.25 ms, while a burst pulse was defined as a broadband signal with an ICI < about 9.25 ms. Individual burst pulses occurred in sequences which contained individual burst pulses that visually and aurally closely matched, including an apparently stereotyped short-long sequence (Chapter IV). I recorded numbers of burst pulse sequences that occurred per feeding interval. For analyses of signal duration, I only included those feeding bouts for which at least 10 signals of a given category occurred.

Behavioral analyses

Video footage was organized according to how clearly I could see the prey ball and nearby dolphin behaviors. Herding and prey-capture behaviors were analyzed only for feeding bouts for which we could see the entire prey ball (except the back side), and dolphin behaviors within 2 m of the prey ball for at least 1 min. Prey-capture behaviors were also analyzed for feeding bouts for which I could see the entire prey ball (except the back side), and all adjacent dolphin behaviors for at least 1 min.

I did individual focal follows on all dolphins that came within 2 m of the prey ball. A herding pass was considered to be the duration of time that a dolphin was within 2 m of the prey ball. The mean length of an adult NZ dusky dolphin (1.73 m, *sensu* Cipriano 1992) was used as a size reference to estimate distance. Herding passes often included prey-capture attempts, which were indicated by a spray of fish away from the dolphin, tilting of the dolphin's head towards the prey ball, or a burst of speed by the dolphin.

For prey-capture attempts, I quantified degree of coordination between individuals according to temporal and spatial synchronicity between individuals doing prey-capture attempts and complementary behaviors (Chapter II). A low level of coordination was considered to include prey-capture attempts that were synchronized temporally (occurred within one second of each other). A medium level of coordination was considered to include prey-capture attempts that were synchronized temporally and spatially. A high level of coordination was considered to include prey-capture attempts that were synchronized temporally and spatially and that exhibited complementary behaviors (Chapter II).

For each feeding bout, the two-dimensional area of prey balls was measured in Image J (http://rsb.info.nih.gov/ij/), with the mean adult length of 1.73 m (Cipriano 1992) used for a size reference. Prey balls were then categorized as small ($< 6\ m^2$) or large. A feeding bout was defined as a continuous, discrete period of feeding.

Statistical analyses

SPSS version 13.0 for Mac software (SPSS Inc., Chicago, IL) was used for analyses. The two-tailed alpha level was set at 0.05. Medians and inter-quartile ranges (IQRs) were used to summarize data because of small sample sizes. I used non-parametric tests (Mann-Whitney U, MW, tests and Spearman's Rank Order correlations, SR) to relate behavioral parameters to signal numbers and parameters. Feeding bouts were considered to be independent since they occurred on different prey balls.

Results

Research effort

A total of 120 1-min intervals from 22 feeding bouts contained high or medium quality signals. I measured prey ball size for all of these bouts. Group sizes were recorded for all but 4 of these 1-min intervals and all but one of these feeding bouts. I analyzed concurrent underwater behaviors for 16 feeding bouts.

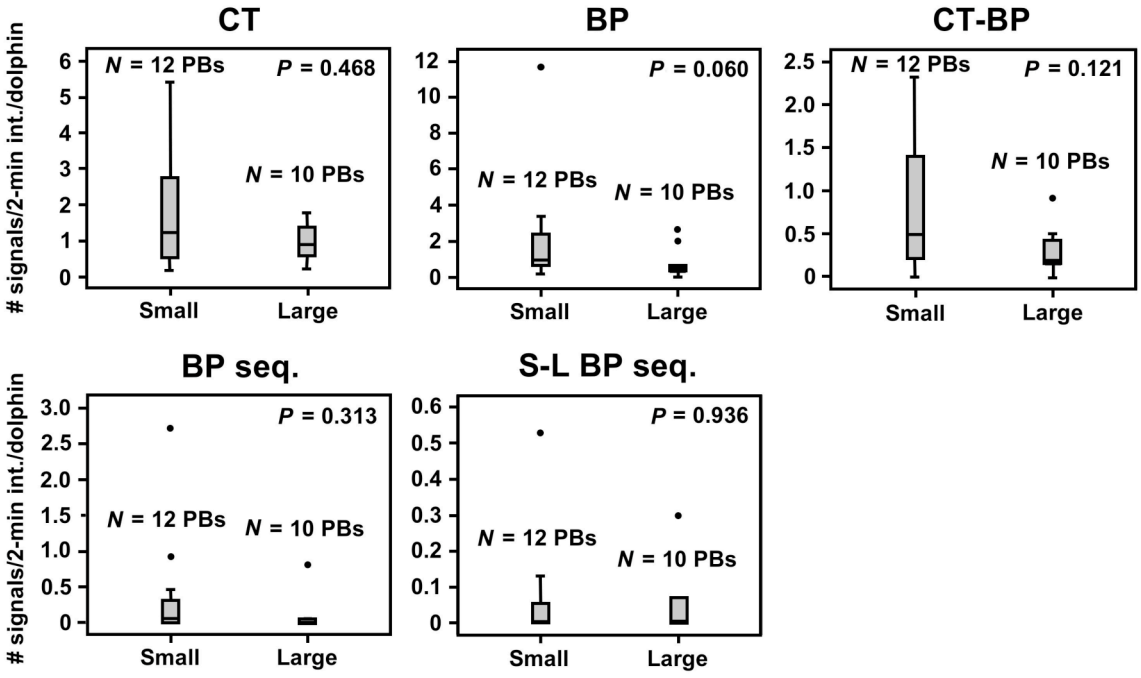

Figure 19. Number of signals in each category per 2-min interval per dolphin in relation to prey ball size (small vs. large). Y-axis scales differ between graphs. CT = click trains, BP = burst pulses, CT-BP = click train-burst pulses, seq. = sequences, S-L seq. = short-long sequences. FB = feeding bout. Significance values are from Mann-Whitney U tests.

Numbers of signals: differences between feeding bouts

Number of signals did not relate to dolphin group size (click trains: $P = 0.249$; burst pulses: $P = 0.533$; click train-burst pulses: $P = 0.702$; burst pulse sequences: $P = 0.485$; short-long burst pulse sequences: $P = 0.485$; SR correlations, $N = 22$ feeding bouts). Number of signals also did not relate to prey ball size (click trains: $P = 0.468$; burst pulses: $P = 0.060$; click train-burst pulses: $P = 0.121$; burst pulse sequences: $P = 0.313$; short-long burst pulse sequences: $P = 0.936$; MW tests, Figure 19).

Numbers of click trains, burst pulses, and click train-burst pulses related positively to number of herding passes, number of prey-capture attempts, and degree of coordination during prey-capture attempts (Table 7). Number of burst pulse sequences also related positively to these herding and prey-capture parameters, but number of short-long burst pulses sequences did not relate to herding or prey-capture parameters.

Chirp-scream burst pulses only occurred during one feeding bout. This was a feeding bout with a large group size for this study (15 dolphins) and the second smallest prey ball (1.5 m^2). This was also the feeding bout that had the highest number of burst pulses (11.67 burst pulses per 2-min interval per dolphin; the second highest was 5.89 burst pulses) and burst pulse sequences (2.73 sequences per interval per dolphin; the second highest number was 1.33 sequences). This feeding bout did not have the highest number of click trains or click train-burst pulses. I was not able to quantify underwater behavioral parameters for this feeding bout because of low visibility, but it was a high activity feeding bout with many prey-capture attempts per interval per dolphin.

Table 7. Numbers of signals from different categories per feeding bout in relation to numbers of prey-capture behaviors, herding behaviors, and prey-capture behaviors that included varying degrees of coordination. Significant correlations are in bold, and are from Spearman's correlations. PC = prey-capture attempt.

	P	**R**	***N***
Click trains			
# PC	**0.003**	**0.698**	**16**
# herding passes	**0.012**	**0.647**	**14**
# PC, no coordination	**0.005**	**0.663**	**16**
# PC, low coordination	0.091	0.436	16
# PC, medium coordination	**0.017**	**0.585**	**16**
# PC, high coordination	**0.041**	**0.516**	**16**
Burst pulses			
# PC	**< 0.001**	**0.862**	**16**
# herding passes	**< 0.001**	**0.815**	**14**
# PC, no coordination	**< 0.001**	**0.881**	**16**
# PC, low coordination	0.271	0.293	16
# PC, medium coordination	**0.002**	**0.723**	**16**
# PC, high coordination	**0.028**	**0.548**	**16**
Click train-burst pulses			
# PC	**< 0.001**	**0.862**	**16**
# herding passes	**< 0.001**	**0.880**	**14**
# PC, no coordination	**< 0.001**	**0.927**	**16**
# PC, low coordination	0.375	0.238	16
# PC, medium coordination	**0.003**	**0.687**	**16**
# PC, high coordination	**0.014**	**0.603**	**16**

Table 7 continued.

	P	**R**	***N***
Burst pulse sequences			
# PC	**0.049**	**0.499**	**16**
# herding passes	**0.049**	**0.534**	**14**
# PC, no coordination	0.118	0.407	16
# PC, low coordination	0.126	0.399	16
# PC, medium coordination	**0.047**	**0.184**	**16**
# PC, high coordination	0.233	0.316	16
Short-long burst pulse sequences			
# PC	0.521	0.173	16
# herding passes	0.835	0.061	14
# PC, no coordination	0.357	0.247	16
# PC, low coordination	0.422	0.216	16
# PC, medium coordination	0.496	0.184	16
# PC, high coordination	0.319	0.266	16

Signal durations: differences between feeding bouts

Signal duration was not related to group or prey ball sizes. Group size did not relate to duration of click trains ($P = 0.124$, $N = 16$ feeding bouts), burst pulses ($P = 0.763$, $N = 14$ feeding bouts) or click train-burst pulses ($P = 0.814$, $N = 9$) (SR correlations). Prey ball size did not relate to duration of click trains ($P = 0.344$, $N = 8$ small and 8 large prey balls) or burst pulses ($P = 0.524$, $N = 10$ small and 4 large prey balls) (MW tests). Duration of some signal categories related to herding and prey-capture behaviors (Table 8).

Table 8. Duration of different signal categories in relation to numbers of prey-capture behaviors, herding behaviors, and prey-capture behaviors that included varying degrees of coordination. Behaviors were analyzed as numbers of behaviors per 1-min interval. Significant correlations are in bold, and are from Spearman's correlations. PC = prey-capture attempt.

	P	**R**	***N***
Click trains			
# PC	0.819	0.078	11
# herding passes	1.000	0.000	8
# PC, no coordination	0.429	0.266	11
# PC, low coordination	0.217	0.405	11
# PC, medium coordination	0.838	-0.070	11
# PC, high coordination	0.447	0.256	11
Burst pulses			
# PC	0.177	0.494	9
# herding passes	0.160	0.548	8
# PC, no coordination	0.110	0.569	9
# PC, low coordination	0.954	-0.023	9
# PC, medium coordination	0.600	-0.203	9
# PC, high coordination	0.907	0.046	9
Click train-burst pulses			
# PC	0.084	0.754	6
# herding passes	0.104	0.800	5
# PC, no coordination	**0.042**	**0.829**	**6**
# PC, low coordination	0.158	0.655	6
# PC, medium coordination	0.499	0.348	6
# PC, high coordination	0.558	0.304	6

Numbers of signals in relation to duration

I related total number of signals per 2-min feeding interval to duration of each signal category to examine the relationship between amount of sound in the underwater environment and signal duration. Number of signals did not relate to duration of click trains ($P = 0.334$, $N = 16$ feeding bouts), burst pulses ($P = 0.813$, $N = 14$ feeding bouts), or click train-burst pulses ($P = 0.546$, $N = 9$ feeding bouts) (SR correlations).

Discussion

What signal categories functioned in prey captures?

The number of prey-capture attempts related positively to number of click trains, burst pulses, click train-burst pulses, and burst pulse sequences. These relationships suggest that all of these signal categories had a prey-capture role, although that role potentially related to echolocating on prey, containing prey, foraging or social communication, or some other role.

There was an insignificant trend ($P = 0.084$) for number of prey-capture attempts to relate positively to duration of click train-burst pulses, which suggests that click train-burst pulses functioned in echolocating on prey. Other delphinids often use signals that contain click train and burst pulse components when they attempt prey captures (Miller et al. 2004; DeRuiter et al. 2009). During the process of echolocating on prey, clicks get closer together as the dolphin approaches the prey (Madsen et al. 2005). Since dolphins continue these signals until they capture a prey item, signal duration may be longer (or shorter) when the dolphin captures prey than when it aborts a prey-capture attempt. Since number of prey-capture attempts did not relate to duration of click trains or burst

pulses, these signal categories likely do not function in echolocating on prey. Instead, at least some burst pulses likely function in foraging communication. For other delphinids, communication is a frequent function of burst pulses (Dudzinski 1996; Herzing 1996; Janik 2009), and low frequency burst pulses used by dusky dolphins have characteristics that you would expect to see in communicative signals (Chapter IV). It is possible that dusky dolphins also use some click trains for communication during foraging (Janik 2009). Alternatively, dolphins may use click trains to monitor their environment or characteristics of a prey ball (Herzing and dos Santos 2004). This monitoring may increase concurrently with prey-capture effort.

What signal categories functioned in herding?

If acoustic signals functioned in herding, one might expect numbers or duration to relate positively to prey ball size, since larger prey balls were harder for dolphins to contain (Vaughn et al. 2010b). Instead, I found a negative relationship between signal numbers and prey ball size, which suggests that dolphins at least do not use at least lower frequency signals to contain prey. When prey balls were small, there was an insignificant trend for there to be twice as many burst pulses per 2-min interval per dolphin as when prey balls were large ($P = 0.06$), and for there to be more than twice as many click train-burst pulses ($P = 0.121$). It is possible that small prey balls were the result of successful low frequency signals; however, this is unlikely since I only saw a prey ball split into smaller prey balls on one occasion, and on this occasion the 2 halves of the (small) prey ball stayed within 4 m of each other. There may have been more

burst pulses and click train-burst pulses when prey balls were small because there was more feeding activity when dolphins fed on smaller prey balls (Chapter II).

Although there were twice as many burst pulses per 2-min interval per dolphin when prey balls were small, there were not more burst pulse sequences when prey balls were small, which suggests that burst pulse sequences may have a social communication role rather than a foraging communication role. For other delphinids, burst pulse sequences have also been hypothesized to have a social communicative role. Burst pulse sequences of northern right whale dolphins were hypothesized to play a role in individual identification (Rankin et al. 2007), and sequences of killer whale calls were hypothesized to be used for communication during close range interactions (Riesch et al. 2008).

If a signal category functioned in herding, one might also expect signal numbers and duration to relate to number of herding behaviors. Number of herding behaviors did relate positively to number of click trains, burst pulses, click train-burst pulses, and burst pulse sequences. However, these relationships paralleled those between number of prey-capture attempts and numbers of signals. There was also an insignificant trend (P = 0.104) for number of herding passes to relate positively to durations of click train-burst pulses, but this trend again paralleled the relationship between number of prey-capture attempts and duration of click train-burst pulses. These parallels suggest that these signal categories do not have herding functions that are independent of their prey-capture functions, but herding and prey-capture functions may be concurrent. The only example that we know of where a delphinid uses signals to contain prey (albeit in a

direct prey-capture context) involves killer whales off Norway using low frequency signals to cause schooling herring to cluster together more tightly prior to stunning the fish with a tail slap (Simon et al. 2006). Dusky dolphins are smaller and more maneuverable than killer whales, and this may allow dusky dolphins to simply use click train-burst pulses to capture prey. I also did not observe the consistent co-occurrence of other signal categories with click-train burst pulses, which would have been indicative of the use of a different signal category in a herding context. However, since more prey captures (Chapter II) and signals occurred when dolphins fed on small prey balls, the sheer number of signals during these feeding bouts may have caused the fish to school together more tightly. I know of no examples where delphinids used acoustic signals to move prey in a particular direction, such as towards the surface. Delphinids might not use signals to move prey because physical behaviors may be more effective for this purpose (e.g., swimming around or under prey balls, Clua and Grosvalet 2001; doing tail slaps at the edges of prey balls, Fertl and Würsig 1995; emitting bubbles, Similä and Ugarte 1993).

What signal categories functioned in communication?

If a signal category functioned in communication, one might expect numbers and duration to relate to dolphin group size. In this study, numbers of signals per category did not relate to group size; however, there was an insignificant trend for duration of click trains to get shorter as group sizes got larger ($P = 0.124$, $R = -0.401$). Dolphins may use click trains with shorter durations as group sizes get larger to reduce chances of masking between click trains of different dolphins (Quick and Janik 2008), or to reduce

the chances of other dolphins eavesdropping on their signals (similar to Janik 2000a; Gregg et al. 2007). These changes in click train durations could occur either if the click trains were used for echolocation monitoring of the environment, or if they were used for communication. I did not find any relationships between total number of signals per 2-min interval and duration of different signal categories, which suggests that the above masking hypothesis is unlikely at this study site.

Similarly, if a signal category functioned in communication, one might expect signal number and duration to relate to degree of coordination during prey-capture attempts. Number of click trains, burst pulses, and click train-burst pulses related positively to numbers of prey-capture attempts that exhibited no, medium, and high coordination. The uniformity of these relationships across all signal categories and most degrees of coordination indicates that these categories have a general prey-capture function, but that they do not specifically facilitate prey captures in more coordinated fashion. Number of burst pulse sequences related positively to number of prey-capture attempts that exhibited a medium degree of coordination, and there were insignificant trend for number of sequences to relate positively to number of prey-capture attempts that included no ($P = 0.118$) or a low ($P = 0.126$) degree of coordination. However, compared to click train, burst pulse, and click train-burst pulse relationships (minimum coefficient for significant correlations = 0.516), burst pulse sequence relationships had low correlation coefficients (coefficient = 0.184 for significant correlation). Burst pulse sequences may function in foraging communication, but it is more likely that they have a

non-foraging role that relates indirectly to foraging coordination, such as social communication.

Duration of click train-burst pulses related positively to number of prey-capture attempts with no coordination, and there was an insignificant trend ($P = 0.110$) for duration of burst pulses to relate positively to number of prey-capture attempts with no coordination. Dusky dolphins may use longer duration click train-burst pulses and burst pulses when there are fewer dolphins immediately around the prey ball (i.e., when prey-capture attempts occur with no coordination between dolphins) for several reasons. Signals that contain click train and burst pulse components often function in a prey-capture role (Miller et al. 2004; Madsen et al. 2005). Using longer click train-burst pulses may allow the dolphin to focus more effectively on a prey item, but this may only be possible when there are fewer dolphins around a prey ball. Or, dolphins may need to use longer click train-burst pulses when they attempt prey captures that involve less coordination between dolphins because individual fish may be more difficult to echolocate onto or capture (Acevedo-Gutiérrez A. 2009; Heithaus & Dill 2009). The latter hypothesis is more likely, since total number of signals did not relate to duration of any signal category. Burst pulses often function in communication (Dudzinski 1996; Janik 2009), and using longer burst pulses when there are fewer dolphins in the immediate vicinity may increase the chances that a communicative signal will be heard by the intended dolphin.

I was not able to relate signal numbers or duration to changes in group sizes during feeding bouts, because I had acoustic data for few feeding intervals during which

group sizes changed. Dusky dolphin feeding bouts in Admiralty Bay and Current Basin were brief in duration (mean = 5 min, SD = 6.2, Vaughn et al. 2007), and group sizes in general changed little during a single feeding bout (mean increase of 1 dolphin per 2-min feeding interval, Vaughn et al. 2010b). Thus, it is unlikely that signals were used to call other dolphins to a feeding bout (Würsig 1986; Acevedo-Gutiérrez and Stienessen 2004), or that characteristics of signals functioned as an indicator of prey and thereby attracted other dolphins (Janik 2000a), at least on the large scale as was reported for large groups of feeding dusky dolphins off Argentina (Würsig and Würsig 1980). However, in this study, since feeding bouts with many prey-capture attempts also included the greatest number of signals, it is possible that these feeding bouts attracted a small number of nearby dolphins. Recording differences between feeding bouts in the number of signals present at the start of feeding compared to rate of increase in dolphins would allow one to test this hypothesis.

For other delphinids, whistles typically function in communication (Dudzinski et al. 2009; Janik 2009), as do chirp-screams (Dudzinski 1996; Herzing 1996). For dusky dolphins in Admiralty Bay and Current Basin, NZ, we observed no clear examples of whistles, but we did observe 3 chirp-scream burst pulses that strongly resembled whistles (Chapter IV). These chirp-screams only occurred during one feeding bout, and this was a feeding bout when there were many dolphins (15) feeding on a small prey ball (1.5 m^2). A high number of prey-capture attempts occurred during this feeding bout, but we were not able to determine how many due to low visibility. Therefore, this appeared to be a good prey ball on which to feed, possibly because it was easier to capture fish

from this prey ball. Due to the high amount of feeding activity and some degree of social behaviors (e.g., rubbing) that occurred, the level of excitement also appeared to be high during this feeding bout. Due to these behavioral variables and because chirp-screams only occurred during one feeding bout, I suggest that these dusky dolphin chirp-screams had a social communicative function rather than a foraging function. This feeding bout also had the highest number of burst pulses and burst pulse sequences per dolphin, and it had more than 3 times as many of each than the feeding bout with the 2nd highest number. In contrast, this feeding bout had only the 14th highest number of click trains and the 3rd highest number of click train-burst pulses. I consequently also suggest that burst pulse sequences and some burst pulses had a social communicative function, whereas click trains and click train-burst pulses had a foraging function.

To my knowledge, there have been no previous studies that examined dusky dolphin burst pulses, and no previous reports of dusky dolphin chirp-scream burst pulses. Dusky dolphin whistles have been reported to occur very infrequently off Kaikoura, NZ (Yin 1999; Au et al. 2010b). However, since these whistles were recorded from groups that contained up to 1000 dolphins and that frequently included common dolphins (Au et al. 2010b), it is not clear if dusky or common dolphins emitted the whistles that were recorded. Further, the whistle-like chirp-screams that we recorded in this study differed markedly from the whistles recorded by Yin (1999). Unlike previously recorded whistles, chirp-screams included harmonics (Yin 1999; Chapter IV), and chirp-screams were of markedly shorter durations and lower frequencies (Yin 1999; Chapter IV).

Conclusions

In conclusion, dusky dolphins appeared to use different signal categories for different purposes during foraging bouts. Click train-burst pulses appeared to be used to echolocate prey, whereas burst pulses and click trains appeared to function indirectly with prey-capture behaviors. Burst pulses appeared to be used for communication. Individual burst pulses more likely functioned in communication relative to foraging coordination, while sequences of burst pulses may have functioned in social communication, or they may simply have been expressions of excitement. The function (s) of click trains were least clear. Dolphins may have used some click trains to communicate or for surveying the environment during foraging. Research that examines which dolphins use what signals, and what behaviors occur subsequent to signals would increase our understanding of signal uses during foraging and in other contexts.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Previous studies on dusky dolphin foraging behaviors have characterized above-water behaviors (Würsig and Würsig 1980; Würsig 1982; Würsig 1986; McFadden 2003; Markowitz et al. 2004; Degrati et al. 2008; Vaughn et al. 2007, 2008) and generally described underwater behaviors (Würsig and Würsig 1980; Vaughn et al. 2008, 2010a). These studies described the coordinated prey herding and capturing behaviors that dusky dolphins use to feed on schooling fishes in shallow bays off NZ and Argentina (Würsig and Würsig 1980; McFadden 2003), and examined the range of seabirds, pinnipeds, and sharks that associate with dolphins during feeding (Würsig and Würsig 1980; Vaughn et al. 2007). They also examined under what conditions dolphins are able to successfully contain schooling fishes (e.g., when group sizes are larger, Würsig and Würsig 1980; when prey balls are smaller, Vaughn et al. 2010b; when fewer diving gannets are present, Vaughn et al. 2010b), and they investigated the role of dusky dolphins in the broader ecosystem by presenting information on how dolphin foraging behaviors increased prey accessibility for seabirds (Vaughn et al. 2008).

Previous studies on dusky dolphin acoustic signals indicate that the majority of their echolocation signals have center frequencies > 90 kHz (Au and Würsig 2004), which suggests that signals in narrowband recordings (e.g., 0-16 kHz) only comprise a portion of their total signal repertoire. Dusky dolphins appear to seldom if ever whistle (Yin 1999), which suggests that they may instead use diverse burst pulses for

communication. Burst pulses of delphinids have been characterized much less often than click trains or whistles, and their proximate functions have been infrequently examined. The burst pulses of dusky dolphins are of particular interest as an example of a potentially non-whistling dolphin that exhibits much coordination during feeding.

The objectives of this dissertation were to build on these previous studies by investigating dusky dolphin underwater bait-balling behaviors and acoustic signals and their proximate functions, and how ecology versus social learning related to these behaviors and signals. Many pelagic and semi-pelagic delphinids are difficult to study due to inaccessibility, unpredictable distributions, or difficulty in observing them underwater due to low visibility or highly mobile behaviors. Here, I had the opportunity to describe and investigate underwater behaviors and concurrent acoustic signals for a relatively accessible semi-pelagic dolphin. The findings from this study are broadly applicable to other delphinids since many species exhibit similar foraging tactics, and at least 14 of 33 species at times herd prey (Wells et al. 1999; Connor 2000; Heithaus and Dill 2009). To analyze dusky dolphin behaviors and acoustic signals, I used about 800 min of underwater video and acoustics recordings made in NZ in 2005-2006, and a dataset of dusky dolphin foraging behaviors and acoustics from Argentina.

Firstly, I investigated dolphin underwater bait-balling behaviors in relation to group and prey ball sizes in NZ and Argentina. Observed herding behaviors consisted of dolphins swimming around or under prey balls with their sides facing prey balls. These behaviors may have facilitated containing prey balls as stationary aggregations at the surface, or moving prey balls towards the surface. While most herding passes occurred

on the sides of prey balls, three times as many passes occurred on the bottom as on the top of prey balls, which may be because dolphins tried to move prey balls to the surface (similar to Würsig and Würsig 1980; Nøttestad et al. 2002). Dolphins in larger groups were more likely to swim under prey balls than dolphins in smaller groups, which may mean that larger groups are more effective at herding prey balls to the surface, as suggested by Würsig and Würsig (1980). When a dolphin attempted to capture prey, it would typically tilt its belly towards the prey ball and capture fish from the side of the prey ball, although dolphins did infrequently swam through prey balls to capture fish. Dolphins were more likely to swim through larger prey balls than they were to swim through smaller prey balls during prey-capture attempts, which suggests that swimming through large prey balls may be a tactic that reduces the confusion effect and thereby makes it easier for a dolphin to focus on individual fish (Norris and Schilt 1988).

Coordinated herding and prey-capture behaviors occurred frequently. Coordinating herding behaviors may have facilitated containing the prey ball (Würsig 1986), or they may have helped non-herding dolphins to capture prey more easily. Coordinated prey captures likely also made it easier for dolphins to capture prey, and these behaviors involved ≥ 2 dolphins attempting prey captures within 1 s of each other. The most highly coordinated prey-capture attempts involved dolphins capturing fish within 1 s and 2 m of each other, and trapping fish between them (similar to Gazda et al. 2005). The most common prey-trapping tactic in Argentina was a converging formation, in which 2 or more dolphins swam directly towards each other. The most common prey-

trapping tactic in NZ was a pinwheel formation, which involved 2 or more dolphins circling around the prey ball in the same direction as they attempted prey captures.

Diverse species coordinate behaviors to contain or capture prey, including terrestrial mammals such as chimpanzees (*Pan troglodytes*, Boesch and Boesch 1989), lions (*Panthera leo*, Caraco and Wolf 1975), and wild dogs (*Lycaon pictus*, Carbone et al. 1997), and diverse marine species such as yellowtail amberjacks (Schmitt and Strand 1982), humpback whales (Clapham 2000), and jackass penguins (*Spheniscus demersus*, Broni 1985). Predators may work together to cut off escape options of prey (Wells et al. 1999), to separate a prey item or part of a fish school so that it is easier to capture (Schmitt and Strand 1982), or to use other specialized prey-capture tactics (e.g., Gazda et al. 2005). Dusky dolphins coordinated behaviors during containment and capturing tactics. Coordination during containment tactics appeared to enhance the ability of dolphins to prevent prey from escaping from a stationary position near the surface. Coordination during prey capturing tactics appeared to make it easier for dolphins to capture prey by trapping prey between dolphins, and thus reducing its escape options at the time of the prey-capture attempt.

Broad similarities in behavioral variations between and within study locations suggest that broad behaviors related to ecology rather than social learning. Dolphin group size related to location of herding passes and body orientation during prey-capture attempts, while prey ball size related to location of prey-capture attempts. Fine-scale differences in behavioral variations between locations suggest that fine-scale behaviors such as group prey-capture formations were more likely due to social learning. Dolphin

Argentina and NZ populations have been separated for over one-half million years (Harlin-Cognato et al. 2007), and these 2 populations likely learned different specialized behaviors for containing and capturing schooling fish (similar to Weinrich et al. 1992).

To examine functions of dolphin prey herding and capturing behaviors, I secondly investigated the relationships between dolphin bait-balling behaviors and prey ball escape behaviors in NZ. I observed horizontal and vertical prey ball escape movements, but the only distinct escape behavior was a rapid downward funneling action of the prey ball (also reported to occur for herring being fed on by killer whales, Nøttestad and Axelsen 1999). Funneling was most likely to occur for large prey balls, and it occurred just before they rapidly descended to depth. Dolphins at times appeared to try to prevent funneling prey balls from descending by swimming under the prey balls, but we were not able to quantify the relative frequency of this behavior due to small sample sizes. Some dolphin behaviors were more likely to occur when prey balls ascended and so may also have prevented prey balls from descending. These behaviors were a greater number of herding passes that did not include a prey-capture attempt, attempting prey captures on the sides rather than by swimming through prey balls, and facing their bellies towards prey balls during prey-capture attempts (also observed for Atlantic spotted dolphins, Fertl and Wursig 1995, and killer whales, Simila and Ugarte 1993).

Broad-scale dolphin herding and prey-capture behaviors thus related to broad-scale prey ball escape behaviors. We did not examine behaviors on a fine-scale, and an investigation of differences in escape behaviors between fish species could provide

further insights into dolphin behavioral differences between NZ and Argentina. Predator feeding tactics co-evolve with prey escape tactics (Krebs and Davies 1993), and one might expect that dolphin behaviors relate not only to contextual parameters such as prey ball size and depth, but also to changes in prey behaviors such as the formation of a prey ball shape that might be expected to precede rapid escape. Other variables also relate to how likely it is that a prey ball will escape, including dolphin group size (Würsig and Würsig 1980) and presence of seabirds (Vaughn et al. 2010b), and a multivariate analysis of the relative costs and benefits of trying to contain prey balls in different ecological contexts would increase our understanding of dolphin decision-making during foraging.

To allow me to investigate proximate functions of acoustic signals during bait-balling, I thirdly characterized dusky dolphin signals in NZ and Argentina. Since I categorized these acoustic signals using narrow-band recordings (0-16 kHz in NZ and 0-24 kHz in Argentina), I also compared a small sample of broadband dusky dolphin recordings to their down-sampled narrowband counterparts, to determine how representative signals in narrowband recordings were of signals in broadband recordings. Only 26% of broadband signals occurred at low frequencies (0-16 kHz). However, signals that occurred at low frequencies did not appear to be simply the low frequency portions of predominantly high frequency signals. Instead, there were many quantitative differences between low and high frequency signals. Low frequency signals had shorter durations, shorter ICIs, lower center frequencies, and smaller 3-dB bandwidths. These parameter differences between low and high frequency signals indicate that dusky

dolphins likely used these signal categories for different purposes. Low frequency signals more likely functioned in communication (Au 2009; Frankel 2009), whereas high frequency signals more likely functioned in echolocation (Dudzinski et al. 2009; Frankel 2009).

I characterized signals in narrowband recordings using distributions of ICIs, since this was the most robust parameter between signals in broadband recordings and their counterparts in down-sampled narrowband recordings. In NZ, a graph of ICIs across all signals revealed a bi-modal distribution, with the modes split at an ICI of about 9.25 ms. In Argentina, a graph of ICIs revealed a uni-modal distribution, but this mode had approximately the same ICI distribution as the first NZ mode. Since 9.25 ms is the approximate ICI that differentiates widely-spaced click trains from closely-spaced burst pulses (Lammers et al. 2004), we categorized signals as click trains, burst pulses, or signals that contained both click train and burst pulse components. I found no whistles among this dataset (unlike Yin 1999), but I did find 3 chirp-scream burst pulses, which spectrographically strongly resembled whistles. Most signals at both locations were click trains or burst pulses, and a smaller percentage of signals contained both click train and burst pulse components. Besides individual signal categories, we also observed sequences of burst pulses (similar to Rankin et al. 2007; Riesch et al. 2008), which contained 2-14 burst pulses that were spaced closely together and that were highly similar visually and aurally. Since dusky dolphins in Admiralty Bay do not appear to whistle, they likely instead use diverse categories of burst pulses such as chirp-screams and sequences for communication, similar to other delphinids (Dudzinski et al. 2009;

Janik 2009). Low frequency click trains and click train-burst pulses are more likely to have foraging-specific functions such as echolocation of fish (Au 2009; DeRuiter et al. 2009; Frankel 2009).

Similar to foraging behaviors, broad similarities in acoustic parameters between locations suggests that ecology rather than social learning related to what broad acoustic signals were used, and proximate functions of those signals. Click trains, burst pulses, and signals that contain both click trains and burst pulses are used by diverse odontocetes (Madsen et al. 2005; DeRuiter et al. 2009; Dudzinski et al. 2009). Chirp-screams (Dudzinski 1996; Herzing 1996) and sequences of burst pulses (Riesch et al. 2008; Rankin et al. 2009) are also used by other delphinids. Fine-scale differences such as variation in burst pulse categories is more likely to relate to social learning mechanisms, and, in this study, the marked differences between locations in number of burst pulses within each sequence may be due to social learning differences (similar to Mercado et al. 2005).

Fourthly, I investigated proximate functions of narrowband signals in greater depth by relating NZ signal numbers and durations to feeding behavioral parameters. All signal categories related positively to number of prey-capture attempts per feeding interval, which indicates that they had a direct or indirect prey-capture role. Click train-burst pulse signals may have had an echolocation function during prey captures (similar to Madsen et al. 2005), since number of prey-capture attempts per interval per dolphin related positively to duration of click train-burst pulses. No signal categories appeared to have herding functions that were independent of their prey-capture functions, since

relationships between signals and herding behaviors paralleled those regarding prey-capture behaviors. However, the large number of signals emitted, especially when many dolphins fed on small prey balls, may have caused fish to cluster together more tightly and therefore facilitated herding or capturing them (Simon et al. 2006). Burst pulses appeared to have a communication role, based on their strong co-occurrence with chirp-screams. Individual burst pulses were more likely to have had a role in foraging-related communication, whereas sequences of burst pulses were more likely to be used for social communication. The role of click trains was ambiguous, but they likely had a navigation or monitoring role (e.g., relative to prey ball characteristics or presence of predators such as sharks, Frankel 2009), and at times may have been used for communication (Janik 2009).

Dusky dolphins used diverse acoustic signals during foraging, and at least some of these signals likely facilitated communication between individuals relative to coordination of prey herding or capturing behaviors. I did not examine use of non-acoustic signals, but it is likely that non-acoustic signals also are involved in communication relative to coordination of foraging behaviors. Examples of potential non-acoustic signals include body tilts (Würsig et al. 1990), bubble emissions (Trudelle 2010), and touching behaviors (Dudzinski et al. 2010). Similarly, non-acoustic behaviors potentially have a role in containing prey. Killer whales use tail slaps to stun fish to make it easier to capture them (Simon et al. 2006), and Atlantic spotted dolphins appear to use tail slaps and breaches to contain prey (Fertl and Würsig 1995). Dusky dolphin body tilts potentially play a similar role, as a result of confusing or scaring fish.

While the behavioral and acoustic studies in this dissertation increase our understanding of underwater foraging behaviors and acoustic signals of this semi-pelagic dolphin, they also lead to further questions. In this dissertation, descriptions of dolphin and prey ball behaviors were limited to relatively near-surface observations (within about 20 m of the surface) that occurred in relatively shallow bay environments (up to 100 m typical depths, Vaughn et al. 2010a). Future studies could use sonar to investigate dolphin and prey ball behaviors at greater water depths, and to describe prey ball behaviors before, during, and after dolphin feeding (similar to Similä 1997; Nøttestad et al. 2002; Benoit-Bird et al. 2004). Studies of dusky and other dolphins in diverse types of environments would also do much to increase our understanding of the relationships between ecology and foraging behaviors. In this dissertation, my examination of signal categories and proximate functions was constrained by the narrow frequency range of the recordings (0-16 kHz and 0-24 kHz), and by not being able to determine which dolphin emitted each signal. Our understanding of signal categories and their functions would be much increased by a study that examined broadband signals across a wider diversity of behaviors (similar to Quick and Janik 2008), and that used multiple hydrophones that allowed one to localize signals and thus to determine which dolphin emitted each signal (similar to Dudzinski et al. 1995; Quick et al. 2008; Au et al. 2010b). It would then be possible to examine behavioral context at smaller scales, for example describing behaviors that preceded and followed different signal categories.

In addition to increasing our understanding of dusky dolphin foraging behaviors and acoustic signals, the studies in this dissertation give us a glimpse of what life is like

underwater for a semi-pelagic dolphin. We often relate most closely to that which we experience directly. When one looks out at an expanse of blue ocean, one's first impression may be that it contains "nothing but flat empty water as far as the eye can see" (Figure 20). This obviously incorrect impression can easily become a conscious or unconscious justification for directly (Ryan et al. 2009) or indirectly (Diaz and Rosenberg 2008) dumping large amounts of wastes into the oceans, using it for naval live-ammunition training (Hatch and Wright 2007), extracting products that are useful to us with relative disregard for the impacts of finding (e.g., seismic exploration, Tyack 2008) or extracting (e.g., fishing involving large amounts of bycatch, Read 2005) that product, or participating in diverse recreational activities with little awareness of or concern for its impact on local marine inhabitants (e.g., high speed boating through manatee, *Trichechus manatus latirostris*, habitat, Jett and Thapa 2010; feeding sharks, *Negaprion acutidens*, so that tourists can glimpse these elusive creatures, Clua et al. 2010). Even if a person is aware of the diversity and importance of life underwater in the oceans, it may seem less important or less tangible simply because they do not experience it as often or as directly as they experience the immediate terrestrial environments in which they live most of their lives.

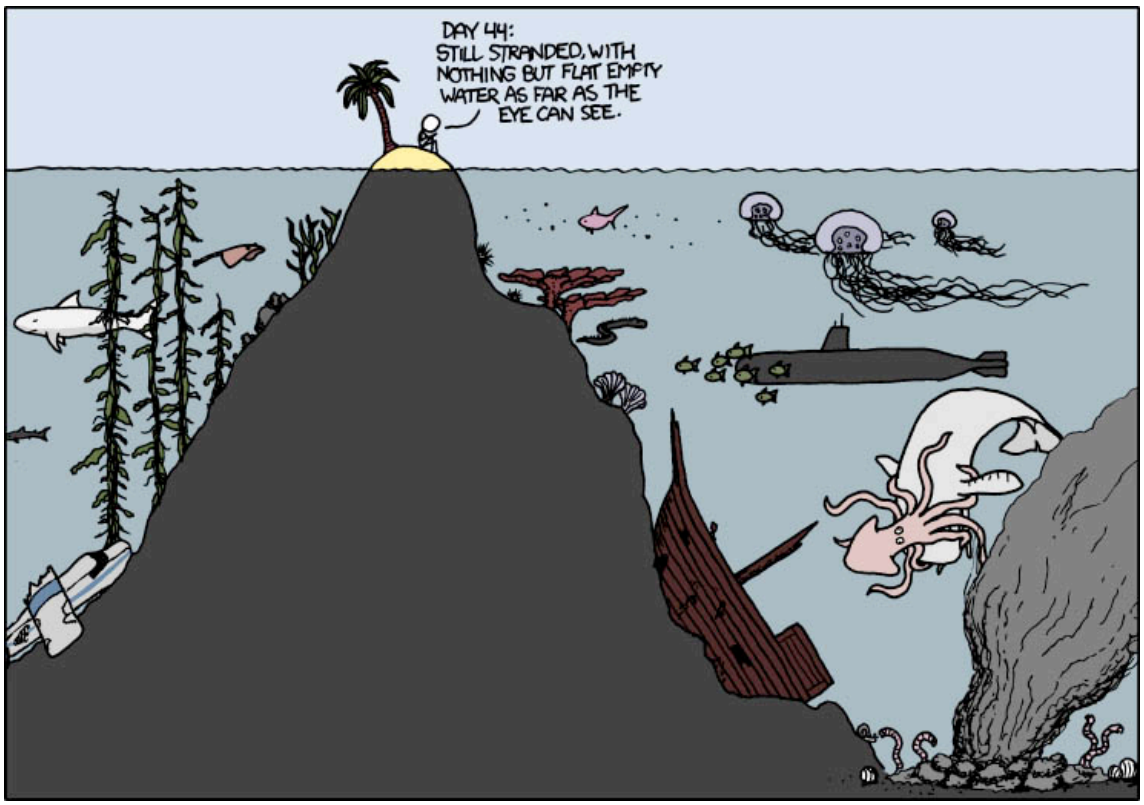

Figure 20. An example of how what you perceive can influence what you see. Reproduced with permission from Munroe 2011.

It is ironic that marine environments at first glance seem to contain less life than do terrestrial environments, and yet, 70% of the surface of the earth is covered by ocean (Thorne-Miller 1999), 99% of the earth's biosphere consists of marine environments (Norse and Crowder 2005), and marine environments contain a broader range of life than do terrestrial environments (Thorne-Miller 1999). Even though humans live primarily in terrestrial environments, the effects that we have on oceans in turn affect us directly and indirectly. Among other functions, oceans have key roles in regulating global carbon cycles, producing oxygen, regulating climate, and feeding a large portion

of the human population (Thorne-Miller 1999). Further, oceans are a source of mystery. An amazing diversity of ecosystems and organism adaptations exist in shallow and deep waters, about which we know comparatively little. This dissertation gives us a brief glimpse of what a semi-pelagic dolphin does during stationary feeding bouts, and how it uses different categories of signals. My hope is that, by sharing this aspect of the underwater environment with others through writing, photography, and videos, that they too will come away with a deeper appreciation for a part of the life that lies under that water, and that this appreciation will translate into conservation action.

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